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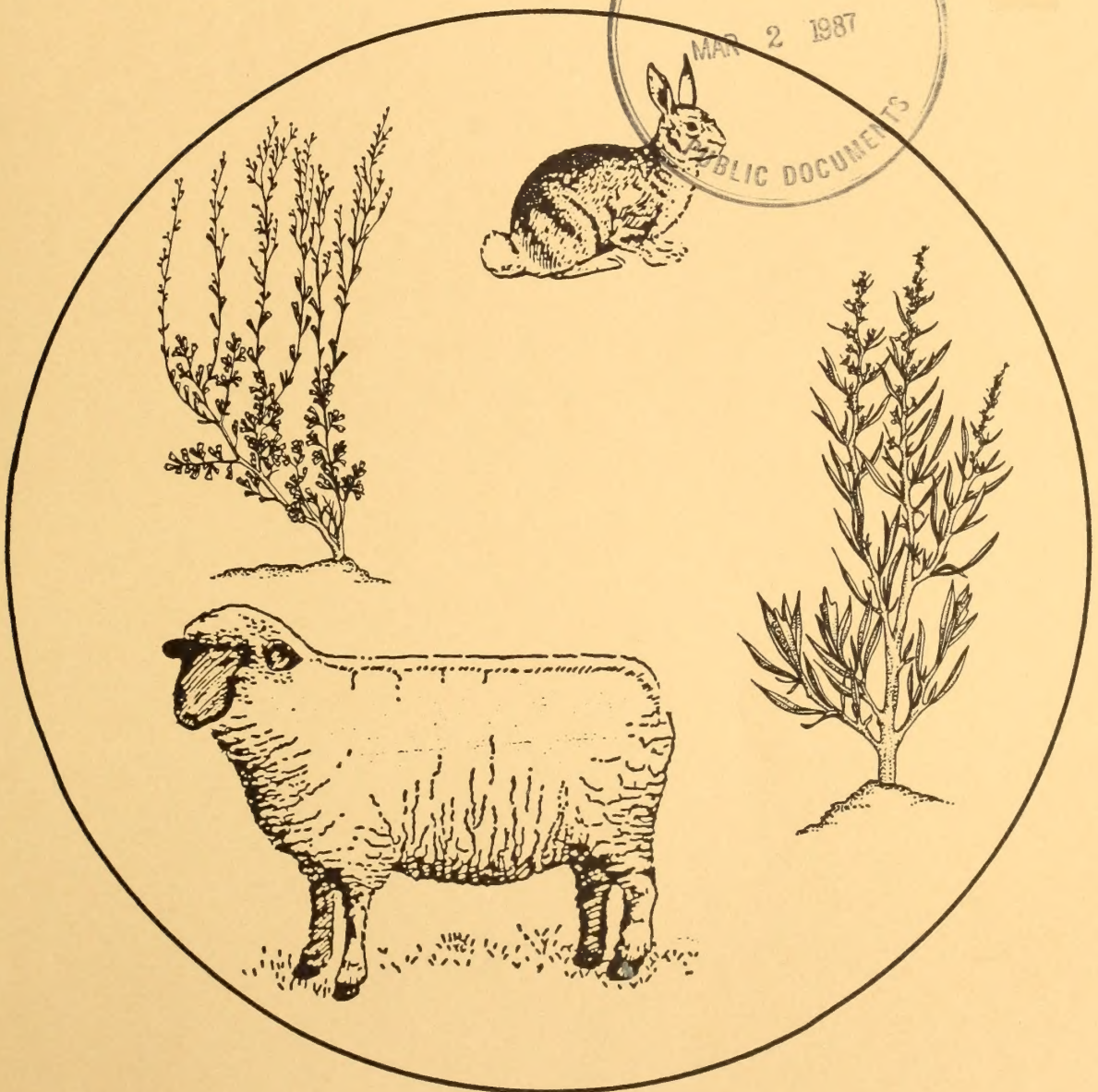
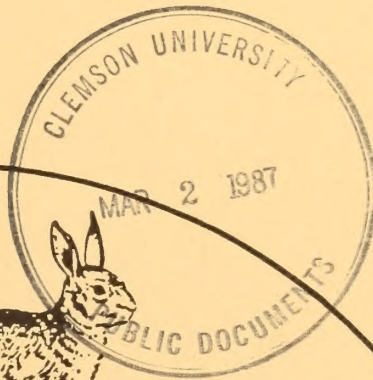
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Proceedings— Symposium on Plant-Herbivore Interactions



Proceedings of the Fourth Wildland Shrub Symposium



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Proceedings—Symposium on Plant-Herbivore Interactions

Snowbird, Utah, August 7-9, 1985

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INTRODUCTION: PLANT-HERBIVORE INTERACTIONS

Frederick D. Provenza, Jerran T. Flinders, and E. Durant McArthur

This proceedings is the fourth in a series on the biology and management of shrubs. Earlier accounts provide information on Purshia, Cowania, and related rosaceous species, on Atriplex and related chenopods, and on Artemisia and Chrysothamnus (Tiedemann and Johnson 1983; Tiedemann and others 1984; McArthur and Welch 1986). All four proceedings have been published by the Intermountain Research Station. The Shrub Research Consortium, whose members are listed inside the front cover of this proceedings, has the continuing role of sponsoring periodic symposia and workshops on shrub biology and management. The symposium described in this volume dealt with plant-animal interactions with emphasis on woody plants and mammalian herbivores.

Plants have typically been considered passive participants in interactions with herbivores. Growing evidence, highlighted in this symposium, suggests that plants play an active role in these interactions, and may deter herbivores through changes in chemistry and morphology. Furthermore, resource availability apparently influences evolution of plant chemical and morphological responses to herbivory, and nutrient availability and light influence their phenotypic expression.

Herbivores, on the other hand, have been viewed as active participants in interactions with plants, because animals are free to select a diet from among the plant species and parts available within plant assemblages. However, people have typically considered that diet selection is genetically fixed through natural selection. The degree to which diet selection is genetically fixed is currently under question for domesticated and wild herbivores, however, and some consider that dietary experiences in early life shape the dietary habits of herbivores for life. If so, this may serve to adapt herbivores to the plant species and parts available within their environment, and may serve to counter, to some degree, the chemical and morphological defenses of plants.

This symposium proceedings addresses these general topics through text and literature citations, and is intended to provide scientists, educators, and wildland managers with current knowledge of plant-herbivore interactions. Because this is a rapidly developing field, many of the ideas presented in the symposium should be viewed as hypotheses that require further testing. We hope, however, that publications such as this will lead to further study, enhanced understanding, and ultimately better management of plants and the herbivores that feed upon them.

ACKNOWLEDGMENTS

As compilers of this symposium proceedings we thank all members of the Shrub Research Consortium for their efforts in making the symposium a success. We especially thank the session chairs: Dr. Jack Brotherson, Dr. Thomas Clausen, Dr. Lee Eddleman, Mr. Norman V. Hancock, Dr. Ron Sosabee, Dr. Darrell N. Ueckert, and Dr. Bruce Welch. Several other individuals also gave extra effort to ensure the success of the symposium and quality of the proceedings. In this regard we note especially Debbie F. Brunson, Roberta L. Powell, Mical Walker, and Tamara D. Smith.

Finally, Brigham Young University Conferences and Workshops personnel were excellent symposium hosts.

REFERENCES

- McArthur, E. Durant; Welch, Bruce L., compilers. Proceedings--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 398 p.
- Tiedemann, A. R.; Johnson, K. L. Proceedings--research and management of bitterbrush and cliffrose in western North America; 1982 April 13-15; Salt Lake City, UT. General Technical Report INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 279 p.
- Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., compilers. Proceedings--symposium on the biology of Atriplex and related chenopods; 1983 May 2-6; Provo, UT. General Technical Report INT-172. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1984. 309 p.

Section 1. Plant Chemistry

EFFECT OF RESOURCE AVAILABILITY ON WOODY PLANT-MAMMAL INTERACTION

John P. Bryant, F. S. Chapin III, T. P. Clausen and P. R. Reichardt

ABSTRACT: The availability of nutrients, light, and water in the environment determine plant resistance to herbivory. Plant carbon/nutrient balance controls the expression of plant chemical defenses. Nutrient stresses cause an increase in carbon-containing defenses such as phenolics, and a decline in nitrogen-containing toxins and deterrents such as alkaloids and nitrates. Light stresses result in the opposite: carbon-based defenses decrease, and as the growth rate is reduced, nitrogen-containing deterrents increase. Fertilization may increase nitrate concentrations, thus decreasing palatability.

INTRODUCTION

A significant recent advance in plant antiherbivore defense theory is the recognition that the availability of resources (mineral nutrients, light, water) in the environment controls plant resistance to herbivory (Janzen 1974; Bryant and others 1983; Coley and others 1985). In ecosystems as diverse as tropical rainforests (Janzen 1974; McKey and others 1981; Coley 1983), subtropical savannas (Cooper and Owen-Smith 1985; Owen-Smith and Cooper, this proceedings), temperate deciduous forests (Rathke 1985), boreal forests (Bryant and Kuropat 1980; Bryant and others 1983), and arctic shrub tundra (Batzli and Jung 1980; Kuropat 1984; MacLean and Jensen 1984) rapidly growing woody plants (often deciduous species) are much more severely grazed than slowing growing woody plants (often evergreen species) (Coley and others 1985, this proceedings).

This relationship between the availability of resources in the environment and plant susceptibility to herbivory is the consequence of two levels of plant response to resource availability. On an ultimate or evolutionary scale, adaptation to low resource levels, resulting in slow intrinsic growth rates (Grime 1977; Chapin 1980), favors selection of strong constitutive defenses in plants. Growth in high resource environments does not (Bryant and Kuropat 1980; Bryant and others 1983; Coley 1983; Coley and others 1985; Coley, this proceedings). On an

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ecological scale, phenotypic responses of plants to nutrient or carbon limitation control a plant's genetic potential to express antiherbivore defense (Bryant and others 1983).

The evolution of plant antiherbivore defense is considered in detail elsewhere in this proceedings (see Coley, this proceedings). Here we discuss the physiological mechanisms whereby woody plant carbon/nutrient balance controls phenotypic expression of plant chemical defenses against herbivory. Although we rely heavily on our own work with the woody plant-snowshoe hare interaction in interior Alaskan boreal forests, we predict that the generalizations we arrive at are common to all woody plant-herbivore interactions.

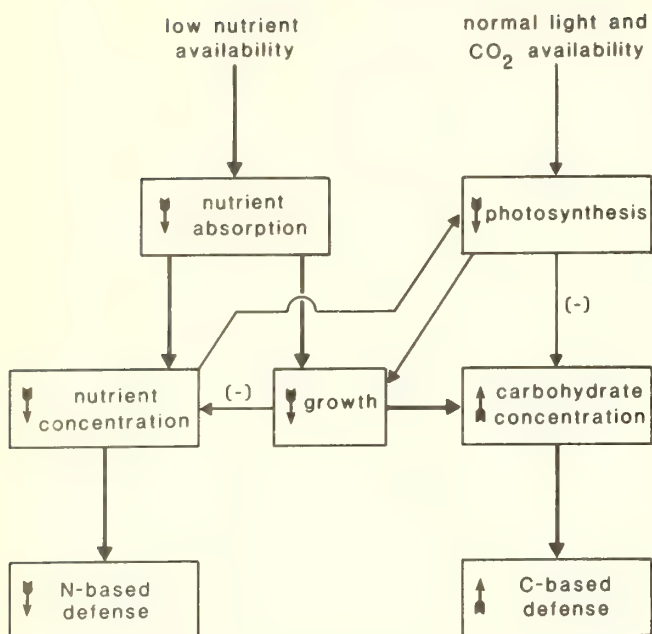
PHENOTYPIC RESPONSE TO NUTRIENT OR CARBON LIMITATION

Bryant and others (1983) suggested that the response of all plants to reduced nutrient availability is qualitatively similar (fig. 1). When nutrients are less available in the soil, less nutrients are absorbed. A reduction in nutrient concentration reduces photosynthetic rate directly by reducing RuBP carboxylase, chlorophyll, and phospholipid contents and indirectly by increasing leaf longevity; older leaves tend to have reduced photosynthetic rates (Mooney 1972; Chapin 1980; Mooney and Gulmon 1982).

Growth is the process most strongly affected by nutrient stress (Chapin 1980). The decline in growth with nutrient stress is generally greater than the decline in photosynthesis; therefore carbohydrates and carbon-based secondary metabolites such as phenols accumulate (Shigo 1973; Wong 1973; McKey 1979). Under conditions of nutrient limitation carbon is relatively "cheap," and the nutrients in leaves are difficult to replace (Bryant and others 1983; Coley and others 1985). Therefore, it is not surprising to see carbon-based defenses such as phenolics increase in woody plant tissues under conditions of nutrient limitation, whereas nitrogen-containing feeding deterrents and toxins such as alkaloids and nitrate decline (Wilde and others 1948; Shigo 1973; McKey and others 1978; Gartlan and others 1980; Waring and others 1985).

The plant phenotypic response to carbon stress due to insufficient light is essentially the reverse of that described above (fig. 1). Photosynthesis and carbohydrate concentrations decline. Growth rate is reduced more severely than nutrient absorption, so that tissue nutrient

Low Nutrients



Low Carbon

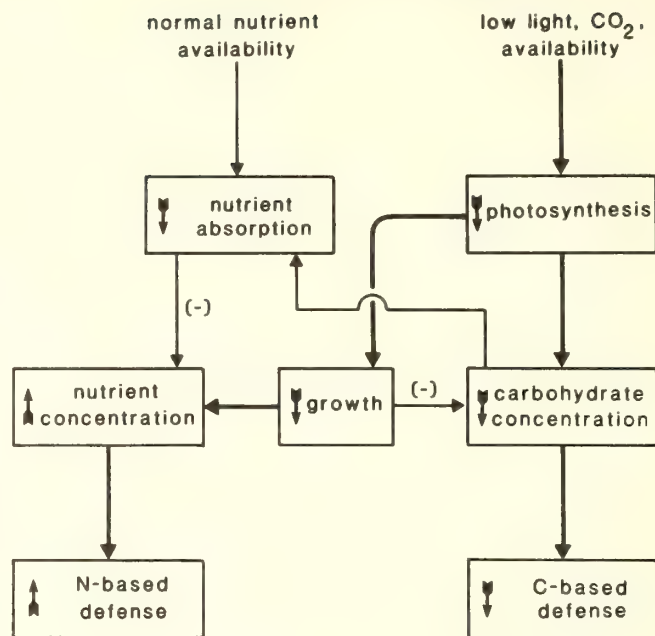


Figure 1.--Effect of suboptimal nutrient or light availability on carbon-nutrient relationships of plants and on concentrations of nitrogen and carbon-based defenses. Vertical arrows within boxes indicate increase or decrease in the parameter. Arrows between boxes indicate positive effect unless otherwise indicated(-). Thickness of arrow indicates magnitude of effect. From Bryant and others (1983).

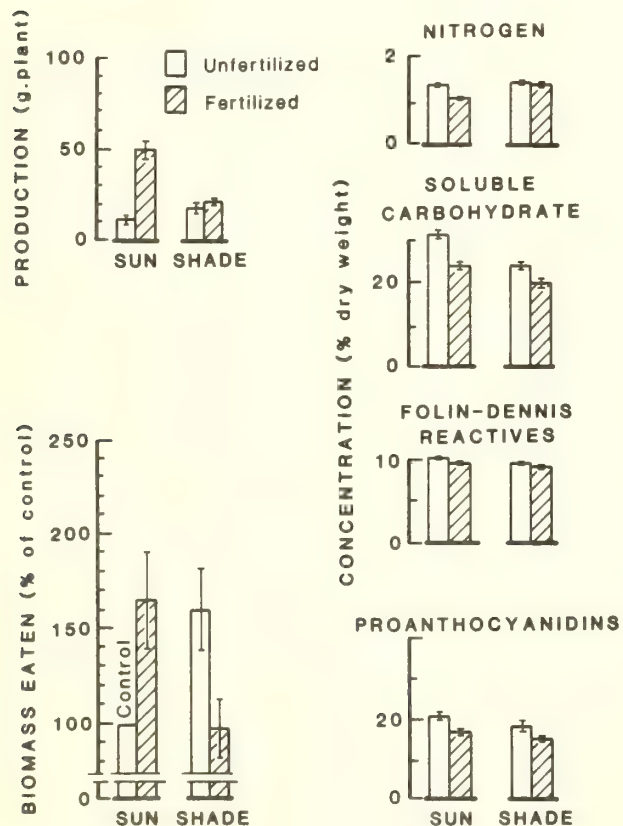


Figure 2.--Effects of fertilization and shading on *S. alaxensis* growth, chemistry, and palatability to snowshoe hares. Mean $1 \pm$ SE presented, N = 30 plants or 10 hares.

concentrations accumulate above levels necessary to support growth. Under such circumstances one finds a reduction in carbon-based defenses such as phenolics and terpenes (Waring and others 1985; figs. 2,3) and in some plants a rise in nitrogen-containing feeding deterrents or toxins (fig. 1) such as nitrate (Deeb and Sloan 1975; Waring and others 1985).

Similarly, following heavy fertilization, tissue nutrient concentrations increase, and growth is stimulated more strongly than photosynthesis; therefore, concentrations of carbohydrates and carbon-based defenses decline and nitrogen-containing feeding deterrents or toxins increase (Cullvenor 1973; Deeb and Sloan 1975; Waring and others 1985).

EFFECTS OF CARBON/NUTRIENT BALANCE ON MAMMAL-WOODY PLANT INTERACTIONS IN BOREAL FORESTS

The palatability of woody plants to browsing mammals is highly sensitive to plant carbon/nutrient balance. For example, fertilization resulted in increased barking and browsing of lodgepole pine (*Pinus contorta*) by snowshoe hares (*Lepus americanus*) and red squirrels (*Tamisciurus hudsonicus*) in British Columbia (Sullivan and Sullivan 1982), snowshoe hare browsing of red pine (*P. resinosa*) in the eastern boreal forest of North America (Heiberg and White 1951), and Scots pine (*P. sylvestris*) by mountain hare (*L. timidus*) in Finland (Rousi 1983). Similarly, fertilization of Scots pine resulted in increased browsing by moose (*Alces alces*) in Finland (Loyttyniemi 1981). The

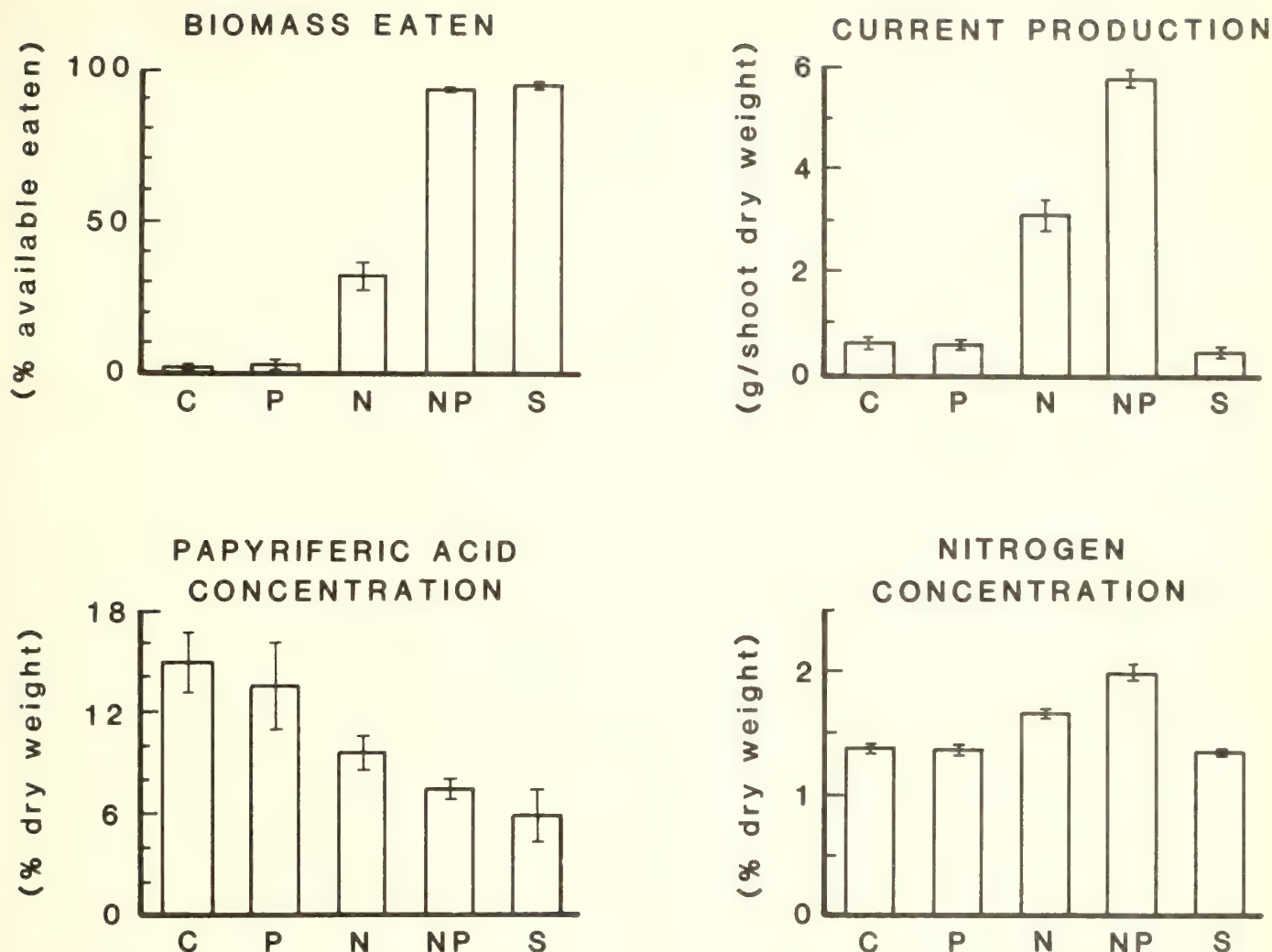


Figure 3.--Effects of fertilization and shading on *B. resinifera* growth, twig nitrogen concentration, papyriferic acid concentration and palatability to snowshoe hares. C = control plants, P = phosphorus-fertilized plants, N = nitrogen-fertilized plants, NP = nitrogen-plus-phosphorus-fertilized plants, S = shaded plants. (Bryant and others, unpublished data)

literature of wildlife ecology and forest management is replete with similar examples of fertilization resulting in increased browsing of woody plants by mammals (see Behrend 1973).

Shading by alder resulted in increased use of a variety of woody plants by snowshoe hares in Alaska (Walker 1985). Rohleder (1985) experimentally demonstrated that Alaska feltleaf willow (*Salix alaxensis*) and balsam poplar (*Populus balsamifera*) grown in shade of alder (*Alnus incana*) are more palatable than *S. alaxensis* and *P. balsamifera* grown in well insolated willow thickets. Waterman and others (1984) found that black colobus monkeys (*Colobus satanus*) fed preferentially on leaves of shaded *Barteria fistulosa* individuals and that those leaves contained lower tannin concentrations than did sun leaves. The extracts from leaves of shaded *B. fistulosa* individuals were also less inhibitory to in vitro digestion of cellulose than extracts from leaves of isolated individuals.

Hanley and others (this proceedings) found that black-tailed deer in southeastern Alaska fed preferentially on shaded shrubs as compared to sun-grown conspecifics. The leaves of shaded shrubs had lower tannin concentrations and higher in vitro digestibilities in deer rumen fluid than those of sun-grown shrubs.

Our experimental studies of forage selection by snowshoe hares in interior Alaska support the generalization that carbon/nutrient balance controls phenotypic expression of plant chemical defense against browsing by mammals. We have grown *S. alaxensis* under high and low mineral nutrition and light in a 2X2 factorial experiment. We applied 40 g N/m² as NH₄NO₃, 20 g P/m² as P₂O₅ and 20 g K/m² as potash in four applications from mid-May to mid-July over a 3 year period and reduced light by 50 percent with optically neutral shade cloth for one growing season. In the winter following the third year of fertilization and first year of

Table 1.--Correlations between *S. alaxensis* chemical fractions¹

Fraction	Fraction							
	N	P	EE	CHO	FD	PA	V	AT
N	1.00							
P	+0.87	1.00						
EE	+0.43	+0.41	1.00					
CHO	-.24	-.03	+0.03	1.00				
FD	+0.12	+0.21	+0.22	+0.79	1.00			
PA	+0.12	+0.22	+0.18	+0.74	+0.91	1.00		
V	+0.18	+0.26	+0.29	+0.67	+0.91	+0.86	1.00	
AT	+0.11	+0.13	+0.23	+0.57	+0.78	+0.74	+0.74	1.00

¹ n = 120, P = 0.01, 118 degrees of freedom = 0.246; N = total nitrogen, P = total phosphorus, EE = diethyl ether extract, CHO = soluble carbohydrate, FD = Folin-Denis, P = proanthocyanidin, V = vanillin, AT = protein precipitating substances.

shading, we bioassayed winter dormant twigs from adult-phase plants (Kozlowski 1979) for palatability to snowshoe hares by offering them in a cafeteria style feeding trial. Twigs were assayed for several nutrient fractions such as nitrogen, soluble carbohydrates, and several phenolic fractions (Folin-Dennis reactives and proanthocyanidins). Fertilization increased growth (fig. 2), thereby indirectly creating a carbon stress that resulted in decreased twig soluble carbohydrate concentrations and phenolic concentrations (fig. 2). Shading directly caused carbon stress, thereby reducing twig soluble carbohydrate and phenolic concentrations (fig. 2). Feeding trials demonstrated that hares fed preferentially on fertilized-only and shaded-only plants ($P < 0.01$) but did not show any preference for fertilized-shaded over control (unfertilized-unshaded) plants (fig. 2).

Correlation analysis of data from this experiment (table 1) demonstrated positive correlations between twig soluble carbohydrate concentrations and concentrations of all phenolic fractions assayed. For example, results presented in figure 4 clearly indicate that a high carbohydrate status results in increased synthesis of potential hare feeding deterrents such as proanthocyanidins. Although these correlative results do not demonstrate, in the absence of preference bioassays where extracts were added to artificial diets (see paper by Reichardt and others, this proceedings), a causal link between low phenolic concentrations in shaded-only and fertilized-only plants, they are suggestive of such a link. Tahvanainen and others' (1985) and Tahvanainen's (this proceedings) demonstration that phenolics deter mountain hare use of willow support this preliminary conclusion. On the other hand, our results with *S. alaxensis* do not indicate that preferential use of *S. alaxensis* winter-dormant twigs is caused by high concentrations of potential feeding attractants such as nitrogen and soluble carbohydrate (figs. 2, 4).

In other experiments with juvenile Alaska paper birch (*Betula resinifera*) (Bryant and others, unpublished) we have arrived at a more definitive demonstration of alteration of plant defense by fertilization and shading. Fertilization increased growth and reduced twig concentrations of a known snowshoe hare feeding deterrent, papyriferic acid (Reichardt and others 1984; this proceedings). Shade reduced growth, increased palatability, and reduced twig papyriferic acid concentration. Again there was no correlation between concentrations of potential feeding attractants and hare use of winter-dormant Alaska paper birch twigs as food (fig. 3).

Results presented in figure 2 indicate that substances other than phenolics may also affect *S. alaxensis*' palatability to snowshoe hares in winter. Twigs of fertilized-shaded plants were less palatable than those of fertilized-only plants or shaded-only plants even though they had the

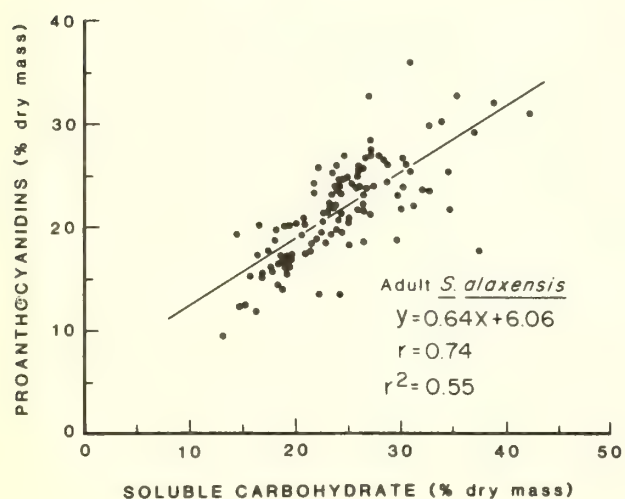


Figure 4.--Relationship between soluble carbohydrate and proanthocyanidin concentrations in winter-dormant twigs of adult-phase *S. alaxensis*. N = 120 plants. r significant at $P < 0.0001$ level of probability.

lowest phenolic concentrations measured in our study of *S. alaxensis*-snowshoe hare interactions. Although our chemical analysis of *S. alaxensis* is still incomplete, preliminary results indicate that twigs of fertilized-shaded plants had a high nitrate concentration compared to twigs of other plants. This high nitrate concentration may be the cause of the low palatability of these twigs to snowshoe hares because nitrate is toxic to vertebrate herbivores, such as rabbits (Deeb and Sloan 1985), that are similar in physiology to hares. However, irrespective of the chemical cause of the low palatability of fertilized-shaded plants relative to fertilized-only and shaded-only plants this result further supports the generalization of Bryant and others (1983). Growth of fertilized-shaded plants was limited by light as compared to that of fertilized-only plants. And furthermore, twigs of fertilized-shaded plants had the highest nitrogen concentration measured in this study (fig. 2). Thus the conditions specified by Bryant and others (1983; see fig. 1) for accumulation of nitrogen containing feeding deterrents or toxins in plants were met.

SUMMARY

A variety of evidence exists that plant palatability to vertebrate herbivores is sensitive to carbon/nutrient balance. Thus the availability of resources in the environment not only influences plant defensive responses to herbivory on an evolutionary scale, it also affects the phenotypic expression of a plant's inherent potential for chemical defense against herbivory. Our results also indicate another aspect of chemical interactions between plants and their herbivore predators. Accumulation of substances such as nitrate that are probably not a direct evolutionary response of plants to herbivore attack may deter vertebrate herbivory. In short, some so-called plant defenses may be "exaptations" (sensu Gould and Verba 1982) rather than adaptations.

REFERENCES

- Batzli, G. O.; Jung, H. G. Nutritional ecology of microtine rodents: resource utilization near Atkasook, Alaska. *Arct. Alp. Res.* 12: 483-499; 1980.
- Behrend, D. F. Wildlife management - forest fertilization relations. In: Forest fertilization. Gen. Tech. Rep. NE-3. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station; 1973: 108-110.
- Bryant, J. P.; Kuropat, P. J. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. *Ann. Rev. Ecol. and Syst.* 11: 261-285; 1980.
- Bryant, J. P.; Chapin, F. S., III; Klein, D. R. Carbon/nutrient balance of boreal woody plants in relation to vertebrate herbivory. *Oikos.* 40: 357-368; 1983.
- Bryant, J. P.; Chapin, F. S., III; Reichardt, P. R.; Clausen, T. P. Effects of shade and mineral nutrition upon the growth and chemical defense of Alaska paper birch and green alder. 1986. Unpublished paper on file at: Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775-0180.
- Chapin, F. S., III. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11: 233-260; 1980.
- Coley, P. D. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53: 209-233; 1983.
- Coley, P. D.; Bryant, J. P.; Chapin, F. S., III. Resource availability and plant antiherbivore defense. *Science.* 22: 895-899; 1985.
- Cooper, S. M.; Owen-Smith, N. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia (Berl.).* 67: 142-146; 1985.
- Culvenor, C. C. Alkaloids. In: Butler, G. W.; Bailey, R. W., eds. Chemistry and biochemistry of herbage. New York: Academic Press; 1973: 375-379.
- Deeb, S. D.; Sloan, L. W. Nitrates, nitrites and health. Bull. 750. Urbana-Champaign, IL: University of Illinois, Agricultural Experiment Station; 1975. 52 p.
- Gartlan, J. S.; Waterman, P. G.; McKey, D. B.; Mbi, C. N.; Struhsaker, T. T. A comparative study of the phytochemistry of two African rainforests. *Biochem. Syst. Ecol.* 8: 401-422; 1980.
- Gould, S. J.; Verba, F. S. Exaptation - a missing term in the science of form. *Paleobiology.* 8: 4-15; 1982.
- Grime, J.P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1194; 1977.
- Heiberg, S. O.; White, D. P. Potassium deficiency of reforested pine and spruce stands in northern New York. *Soil Sci. Soc. Amer. Proc.* 15: 309-376; 1951.
- Janzen, D. H. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica.* 6: 69-103; 1974.
- Kozlowski, T. T. Growth and development of trees. Vol. 1. New York: Academic Press; 1971. 462 p.
- Kuropat, P. J. Foraging behavior of caribou on a calving ground in northwestern Alaska. Fairbanks, AK: University of Alaska; 1984. Thesis.

- Loyttyniemi, K. Nitrogen fertilization and nutrient contents in Scots pine in relation to the browsing preference by moose (*Alces alces*). *Folia For. (Helsinki)*. 487: 1-14; 1981.
- MacLean, S. F.; Jensen, T. J. Food plant selection by insect herbivores: the role of plant growth form. *Oikos*. 44: 211-221; 1984.
- McKey, D. The distribution of secondary compounds within plants. In: Rosenthal, G.A.; Janzen, D. H., eds. *Herbivores: their interaction with secondary plant metabolites*. New York: Academic Press; 1979: 55-133.
- McKey, D. B.; Gartlan, J. S.; Waterman, P. G.; Choo, G. M. Food selection by black colobus monkeys (*Colobus satanus*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 16: 115-146; 1981.
- McKey, D.; Waterman, P. G.; Mbi, C. N.; Gartlan, J. S.; Struhsaker, T. T. Phenolic content of vegetation in two African rain forests: ecological implications. *Science*. 202: 61-63; 1978.
- Mooney, H. A. The carbon balance of plants. *Annu. Rev. Ecol. Syst.* 3: 315-346; 1972.
- Mooney, H. A.; Gulmon, S. L. Constraints on leaf structure and function in reference to herbivory. *Bioscience*. 32: 198-206; 1982.
- Rathcke, B. Slugs as generalist herbivores: tests of three hypotheses on plant choice. *Ecology*. 66: 828-836; 1985.
- Reichardt, P. B.; Bryant, J. P.; Clausen, T. P.; Wieland, G. Defense of winter-dormant Alaska paper birch against Snowshoe hare. *Oecologia (Berl.)*. 65: 58-59; 1984.
- Rohleder, R. J. Behavioral interactions and food preferences of snowshoe hares in winter. Fairbanks, AK: University of Alaska; 1985. Thesis.
- Rousi, M. Susceptibility of pine to mammalian herbivores in northern Finland. *Silv. Fenn.* 17: 301-312; 1983.
- Shigo, A. L. Insect and disease control: forest fertilization relations. In: *Forest fertilization*. Gen. Tech. Rep. NE-3. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station; 1973: 117-121.
- Sullivan, T. P.; Sullivan, D. S. Influence of fertilization on feeding attacks to lodgepole pine by snowshoe hares and red squirrels. *For. Chron.*: 263-266; 1982.
- Tahvanainen, J.; Helle, E.; Julkunen-Titto, R.; Lavola, A. Phenolic compounds of willow bark as deterrents against feeding by mountain hare. *Oecologia (Berl.)*. 65: 319-323; 1985.
- Walker, L. R. The processes controlling primary succession on an Alaskan floodplain. Fairbanks, AK: University of Alaska; 1985. Thesis.
- Waring, R. H.; McDonald, A. J. S.; Larsson, S.; Ericsson, T.; Wiren, A.; Arwidsson, E.; Ericsson, A.; Lohammar, A. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. *Oecologia (Berl.)*. 65: 157-160; 1985.
- Waterman, P. G.; Ross, J. A. M.; McKey, D. B. Factors affecting levels of some phenolic compounds, digestibility, and nitrogen content of the mature leaves of *Barteria fistulosa* (Passifloraceae). *J. Chem. Ecol.* 10: 387-401; 1984.
- Wilde, S. A.; Nulbandov, O. G.; Yu, T. M. Ash, protein and organo-solubles of jack-pine seedlings in relation to soil fertility. *J. For.* 46: 829-831; 1948.
- Wong, E. Plant phenolics. In: Butler, G. W.; Bailey, R. W. eds. *Chemistry and biochemistry of herbage*. New York: Academic Press; 1973: 265-316.

FOREST STAND-AGE-RELATED DIFFERENCES IN APPARENT NUTRITIONAL QUALITY
OF FORAGE FOR DEER IN SOUTHEASTERN ALASKA

Thomas A. Hanley, Rex G. Cates, Beatrice Van Horne, and Jay D. McKendrick

ABSTRACT: Chemical composition of Alaska blueberry (Vaccinium alaskensis) and bunchberry dogwood (Cornus canadensis) was studied during May through October along a chronosequence of five stands of Sitka spruce (Picea sitchensis)-western hemlock (Tsuga heterophylla) forest. Three young stands were open clearcuts; two older stands had well-developed overstories and understories exposed to little direct sunlight. Pronounced differences in chemical composition of blueberry and bunchberry occurred between the young and older stands. Plants in the young stands had greater astringency, concentrations of phenolics, and total nonstructural carbohydrates, but lower concentrations of nitrogen than did plants in the older stands. In vitro dry-matter digestibility, however, did not differ among stands. Chemical analyses of plants from a clearcut and adjacent forest at another study area indicated that concentrations of digestible nitrogen were 2.0 to 2.3 times greater in leaves from the forest than those from the clearcut. Palatability trials with three captive black-tailed deer (Odocoileus hemionus sitkensis) showed a consistent preference for leaves from the forest. The results indicate the carbon/nutrient balance of these plants, controlled by the relative availability of light and nutrients in their environment, has major implications for nitrogen availability to deer but may be less important for the availability of digestible energy.

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INTRODUCTION

In the coastal coniferous forests of the Pacific Northwest, British Columbia, and southeastern Alaska, the theoretical linkage between deer populations and their habitat has long centered on the dramatic changes in forage quantity as stands age (Cowan 1945; Einarsen 1946a; Brown 1961; Gates 1968; Jones 1974; Wallmo and Schoen 1980; Hanley 1984). The quantity of forage is generally greatest in young, open stands, least in closed-canopy even-aged stands, and intermediate in uneven-aged, old-growth stands, depending on snow conditions. Quantity of available forage is important to habitat selection by individual deer and the numerical response of deer populations. Stand-age-related differences in the quality of forage are, however, less well understood and have generally been assumed to be less important than the differences in forage quantity. The few studies from coastal Oregon through Alaska have centered primarily on nitrogen concentration in a few key forage species and have generally indicated slightly greater concentrations of nitrogen in plants growing under forest canopies than in those growing in open clearcuts or burns (Brown 1961; Billings and Wheeler 1979; Rochelle 1980; Van Horne 1982; Ellis 1984), although Einarsen (1946b) reported the opposite. The implications of such differences have remained unclear, however, because the concentration of nitrogen is only one of several factors determining protein availability to deer. Furthermore, nitrogen is only one of many nutritional factors important to deer.

Klein's (1964, 1965) work in southeastern Alaska illustrated the importance of forage quality and nutrition to the growth rates and body sizes of individual deer and the productivity of deer populations. More recently, studies of food intake and foraging energetics of deer (Wickstrom and others 1984) and potential nutritional limitations for deer in southeastern Alaska (Hanley and McKendrick 1983, 1985) also have indicated the importance of forage quality, especially for reproductive females. To an individual mule or black-tailed deer (Odocoileus hemionus), the quality of available forage appears to be much more important than the quantity of forage at all but extremely low levels (<100 kg/ha) of forage availability (Wickstrom and others 1984). Although forage quantity is undoubtedly a critical factor controlling carrying capacity and potential

population levels of deer, forage quality appears to be the more important factor affecting habitat selection and the nutrition of individual deer, at least for black-tailed deer in southeastern Alaska. The nutritional factors of greatest importance in southeastern Alaska appear to be digestible energy, nitrogen, and phosphorus (Hanley and McKendrick 1983).

In 1982-83, we conducted a study of stand-age-related differences in the chemical composition of five major understory species in southeastern Alaska. The results (in preparation) indicated some differences of potentially major significance for herbivores. The purpose of this paper is to examine a subset of those data in relation to their importance to Sitka black-tailed deer (*O. h. sitkensis*). The two most important species to deer, Alaska blueberry (*Vaccinium alaskensis*) and bunchberry dogwood (*Cornus canadensis*), are examined here. Of the laboratory analyses, only the neutral and acidic phenolics, astringency, total nonstructural carbohydrates (TNC), nitrogen (N), phosphorus (P), and *in vitro* dry-matter digestibility (IVDMD) are reported here. To relate these results to deer, we supplemented the data with detergent analyses, estimates of nitrogen digestibility, and palatability trials in 1985. The data indicate that the carbon/nutrient balance of these plants, controlled by the relative availability of light and nutrients in their environment, may determine their leaf concentrations of phenolics, total nitrogen, digestible nitrogen, and palatability to deer.

STUDY AREA AND METHODS

Study Area

The coastal forests of southeastern Alaska are dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) with much lesser amounts of western redcedar (*Thuja plicata*), Alaska yellow-cedar (*Chamaecyparis nootkatensis*), and lodgepole pine (*Pinus contorta*), the latter almost exclusively confined to muskegs. Chichagof and Douglas Islands (approximately 58° N. latitude, 134-135° W. longitude), where this study was conducted, are above the northern limit of the range of western redcedar. Characteristic understory species are blueberries (*Vaccinium alaskensis*, *V. ovalifolium*, *V. parvifolium*), rusty menziesia (*Menziesia ferruginea*), devilsclub (*Oplopanax horridum*), skunk cabbage (*Lysichiton americanum*), bunchberry dogwood, trailing bramble (*Rubus pedatus*), laceflower (*Tiarella trifoliata*), and associated plants (Hult  n 1968). Climate is characterized by cool summers ($\approx 15^{\circ}\text{C}$), generally mild winters ($\approx 0^{\circ}\text{C}$), and precipitation year-around ($\approx 150\text{--}500\text{ cm}$ annually). Wildfire is uncommon; windthrow and clearcut logging are the principal agents of large-scale disturbance. Secondary succession following windthrow or logging characteristically proceeds through a shrub-dominated stage during the first 20 years, to a dense, closed-canopied,

even-aged forest with very depauperate understory for the next 100 or more years, to an uneven-aged old-growth condition after 200 or more years. Annual aboveground production of understory during this successional sequence ranges from as high as 5 500 kg/ha at about 20 years to as low as 0 kg/ha at 50 years (Alaback 1982).

The 1982-83 Data

Chemical composition (neutral and acidic phenolics, TNC, N, and P), astringency, and IVDMD of Alaska blueberry and bunchberry dogwood were studied along a chronosequence of five stands in the Kennel Creek drainage of Chichagof Island: a 5-year-old burned clearcut; a 5-year-old unburned clearcut; an 11-year-old unburned clearcut; an 80-year-old closed-canopy, even-aged stand; and an uneven-aged, old-growth stand (> 450 years old?). The three youngest stands were shrub-dominated, open stands, while the two oldest stands had well-developed forest overstories. On each of three dates (October 20-22, 1982, May 18-19, 1983, and July 26-28, 1983) samples of leaves were collected for analysis. Three samples of each of the two species were collected from each of the five stands. Each sample was a composite obtained from three or more individual plants. Samples were chosen to minimize phenological differences among stands at any one date. In this way, all samples of either species were close to the same phenological stage in growth and development, regardless of which stand they came from. Half of each sample was placed on dry ice immediately and kept frozen at -85°C until analysis for phenolics and astringency. The other half was oven-dried at 40°C for 72 hours, ground in a mill with 20-mesh screen, and oven-dried at 50°C immediately preceding analysis for TNC, N, P, and IVDMD.

Neutral and acidic phenolics were measured using a Waters high pressure liquid chromatograph (HPLC). Detection was at 254 nm and 214 nm using a Model 480 LC Lambda-Max spectrophotometer and a Model 441 Spectrophotometer in series. Gradient reverse phase chromatography was performed as follows: column--Rainin Microsorb C 18, short one; solvent--(A) 2 percent acetic acid, (B) methanol/water/butanol/acetic acid (25:68:50:2); gradient--7 minutes isocratic at 30 percent B followed by 25 minutes linear gradient from 30 percent to 100 percent B; flow rate-- 1 mL/min; absorption range-- 0.2; detection--254 nm and 214 nm in series. The counts per milligram were totaled as an index of concentration of neutral and acidic phenolics for each sample.

Astringency was measured using precipitation of trypsin by tannic acid after the sample was ground under liquid nitrogen and extracted in 50 percent methanol. Protein content was determined from a 0.5-mL aliquot using the Bio-Rad assay (Bradford 1976). The assay was calibrated by precipitation of trypsin (2 mg per mL) with tannic acid (from 0.2 to 1.0 mg/mL). Data were expressed as milligrams equivalent tannic acid

per gram dry weight. Details of the HPLC-phenolic and astringency methods are outlined in McElroy (1984).

Total nonstructural carbohydrates (sugars and starches) were measured using Technicon autoanalysis (Technicon Industrial Systems 1976) on reducing sugars following enzyme extraction with Mylase 100 (Smith 1969, 1979).

Nitrogen and phosphorus concentrations were measured simultaneously on a Technicon Auto Analyzer II (Isaac and Johnson 1976; Hanley and McKendrick 1983).

In vitro dry-matter digestibility was determined using the Tilley and Terry technique (Goering and Van Soest 1970). Rumen fluid was obtained from dairy cattle on high-quality grass hay. Incubation time was 48 hours.

The data were analyzed for statistical significance in a 5 (stands) by 3 (sampling dates) factorial analysis of variance (ANOVA), fixed model. An alpha level of 0.05 was used as the criterion of significance in testing the null hypotheses of no treatment or interaction effects. Each of the composite samples of each species from each stand at each date was treated as a replicate in the experiment rather than a subsample. This permitted us to use ANOVA to identify important differences between stands and dates. Our scope of inference, however, is limited to these five particular stands. Scheffe's multiple comparison procedure (Sokal and Rohlf 1981) was used for comparison of means when ANOVA indicated significant differences.

The 1985 Data

Fiber composition (detergent analysis), IVDMD, estimates of nitrogen digestibility, and relative palatability of Alaska blueberry and bunchberry dogwood were studied in an 8-year-old unburned clearcut and adjacent uneven-aged, old-growth forest on northern Douglas Island during July. Palatability trials required daily collection of forage and necessitated working near our captive deer facility in Juneau. The Kennel Creek study site was prohibitively remote.

Leaf samples of Alaska blueberry and bunchberry dogwood were collected from the clearcut and from the forest on July 5. Both samples of each species were composites, coming from more than 10 individual plants. The samples were oven-dried at 40 °C for 72 hours and ground in a mill with 20-mesh screen. Sequential detergent analyses were conducted following the procedures of Goering and Van Soest (1970) as modified by Mould and Robbins (1982). IVDMD was determined with the Tilley and Terry technique (Goering and Van Soest 1970) using rumen fluid from dairy cattle on high-quality grass hay and incubating for 48 hours. Estimates of nitrogen digestibility were obtained by measuring Kjeldahl N concentration and the astringency of the plant material with bovine serum albumin (Martin and Martin 1982, with modifications): the N concentration provided

an estimate of N digestibility for phenolic-free forages; and the astringency was used to correct that estimate for phenolic-rich forages by predicting the degree of depression of N digestibility (C. T. Robbins and others, in press).

Relative palatability trials for Alaska blueberry from the clearcut versus the forest were conducted with three captive, yearling Sitka black-tailed deer, (two males and one female). Leaves were collected daily and offered to each deer, housed separately, as an ad libitum supplement to their regular commercial diet, which also was offered ad libitum. Leaves were refrigerated in plastic bags overnight and weighed into feeding trays for each deer. Trays were kept filled throughout the day, emptied in late evening and contents weighed to determine daily consumption. A 5-day pretrial preceded the 6-day trial (July 1-6). Assignment of trays for each deer was determined by a flip of a coin and was maintained throughout the pretrial and trial until the last day, when the clearcut leaves were offered in the forest tray and vice versa. All data were corrected to oven-dry weight (100 °C).

No statistical analyses were performed on the 1985 data because sample sizes were small and the purpose of the data was simply to aid interpretation of the earlier chemical results.

RESULTS AND DISCUSSION

Analyses of samples from the chronosequence at the Kennel Creek study area (table 1) indicated a similar pattern for both blueberry and bunchberry: concentrations of carbon-rich compounds (phenolics, astringency, TNC) tended to be greater in plants from the three young, open stands than in those from the two older, forested stands; and concentrations of nutrients tended to be greater in plants from the two older stands than in those from the three younger stands. IVDMD, however, did not vary across stands. Treatment means did not differ among plants from the three younger stands or among plants from the two older stands. The patterns of carbon-rich compounds (phenolics, astringency, and TNC) may result from differences in the availability of light. Under the low light conditions of the forest, understory plants may have reduced photosynthesis. This results in low levels of carbohydrates, growth, and production of carbon-based secondary compounds compared to plants from the open sites. Similar patterns in the production of phenolics, terpenes, and carbohydrates have been shown when light is limiting or when plants are growing under environmental stresses that limit photosynthesis (Rhoades 1979; Bryant and others 1983, this proceedings; Cates and others 1983; Waring and others 1985; Larsson and others, in press). The data for bunchberry are intermediate in this respect in the 11-year-old stand, because many of the plants were shaded by tall, dense shrubs. Similarly, samples from the old-growth stand reflected a variety of microsites differing in their exposure to sunflecks.

Table 1.--Chemical composition, astringency, and *in vitro* dry-matter digestibility (IVDMD) of *Vaccinium alaskensis* and *Cornus canadensis* leaves collected from five stands on three dates at the Kennel Creek study area

Variable/species/month	Stand age (years)					$\bar{x}$
	5 (burn)	5	11	80	>450	
Neutral and acidic phenolics (counts/mg)						
<i>V. alaskensis</i>						
May	9,807	10,151	10,685	3,323	4,523	6,566 ^a
July	9,080	10,671	10,890	750	1,439	7,195 ^a
October	9,621	10,594	10,088	798	4,873	7,698 ^a
$\bar{x}$	9,503 ^b	10,472 ^b	10,555 ^b	1,624 ^c	3,612 ^c	
<i>C. canadensis</i>						
May	23,448	15,677	14,143	1,899	4,008	11,928
July	26,189	22,794	7,415	1,265	1,976	9,665
October	13,565	23,153	5,725	2,035	3,846	11,835 ²
$\bar{x}$	21,067	20,541	9,094	1,733	3,277	***
Astringency (mg/g tannic acid equivalent)						
<i>V. alaskensis</i>						
May	4.25	1.35	0.82	0.11	0.36	1.38 ^a
July	3.02	1.81	4.38	0.42	1.84	2.30 ^{a, b}
October	3.54	3.80	6.49	2.53	1.03	3.48 ^b
$\bar{x}$	3.61 ^c	2.32 ^c	3.90 ^c	1.02 ^c	1.08 ^c	
<i>C. canadensis</i>						
May	7.76	7.56	6.67	6.94	6.44	7.07 ^{a, b}
July	10.77	8.36	8.16	4.96	3.95	7.24 ^b
October	6.59	9.46	4.85	2.72	3.62	5.45 ^a
$\bar{x}$	8.38 ^c	8.46 ^c	6.56 ^{c, d}	4.87 ^d	4.67 ^d	
Total nonstructural carbohydrates (percent)						
<i>V. alaskensis</i>						
May	24.3	24.3	26.7	18.4	19.6	22.7 ^a
July	17.9	14.9	15.4	5.7	10.6	12.8 ^b
October	13.2	15.2	15.9	6.8	7.8	11.8 ^b
$\bar{x}$	18.3 ^c	18.1 ^c	19.3 ^c	10.3 ^d	12.7 ^d	
<i>C. canadensis</i>						
May	8.3	10.5	9.8	5.1	6.3	8.0 ^a
July	11.7	10.7	11.5	5.4	4.7	8.8 ^a
October	8.3	10.7	9.0	4.7	6.1	7.8 ^a
$\bar{x}$	9.4 ^b	10.6 ^b	10.1 ^b	5.1 ^c	5.7 ^c	
Total nitrogen (percent)						
<i>V. alaskensis</i>						
May	5.77	4.68	5.20	6.64	6.66	5.79
July	2.02	2.06	1.90	2.72	2.46	2.23
October	1.23	1.55	1.19	1.64	2.08	1.54
$\bar{x}$	3.01	2.76	2.76	3.67	3.73	***
<i>C. canadensis</i>						
May	3.69	3.44	3.43	4.12	4.05	3.75 ^a
July	2.02	1.68	1.62	1.89	1.89	1.81 ^b
October	1.60	1.70	1.59	1.85	1.80	1.71 ^b
$\bar{x}$	2.44 ^{c, d, e}	2.27 ^{d, e}	2.21 ^e	2.61 ^c	2.58 ^{c, d}	

(continued)

(continued)

Table 1. Continued

Variable/species/month	Stand age (years)					$\bar{x}$
	5 (burn)	5	11	80	>450	
Total phosphorus (percent)						
<u>V. alaskensis</u>						
May	0.78	0.71	0.81	0.89	0.85	0.81 ^a
July	0.23	0.26	0.25	0.27	0.24	0.25 ^b
October	0.11	0.12	0.12	0.21	0.13	0.14 ^c
$\bar{x}$	0.38 ^{d,e}	0.37 ^d	0.39 ^{d,e}	0.46 ^e	0.41 ^{d,e}	
<u>C. canadensis</u>						
May	0.55	0.61	0.67	0.72	0.64	0.64
July	0.29	0.34	0.37	0.34	0.27	0.32
October	0.24	0.20	0.27	0.27	0.18	0.23
$\bar{x}$	0.36	0.38	0.44	0.44	0.36	***
IVDMD (percent)						
<u>V. alaskensis</u>						
May	69.0	64.3	67.3	71.1	69.1	68.1 ^a
July	46.4	41.9	43.8	41.1	43.8	43.4 ^c
October	46.1	47.9	51.2	45.6	52.1	48.6 ^b
$\bar{x}$	53.8 ^d	51.4 ^d	54.1 ^d	52.6 ^d	55.0 ^d	
<u>C. canadensis</u>						
May	61.2	69.0	67.6	74.4	66.5	67.8 ^a
July	69.3	62.2	57.3	62.1	55.3	61.2 ^b
October	58.4	66.1	56.9	57.5	57.2	59.2 ^b
$\bar{x}$	63.0 ^c	65.8 ^c	60.6 ^c	64.7 ^c	59.7 ^c	

¹ Means superscripted with the same letter are not significantly different at $\alpha = 0.05$.

² A triple asterisk in the last row, last column indicates a significant interaction at the $\alpha = 0.05$ level between month and stand.

The pattern of nitrogen concentration being greater in the forests than the clearcuts was similar to that reported by other investigators (Billings and Wheeler 1979; Van Horne 1982; Rose 1982) and appears to be consistent throughout these coastal forests. Phosphorus exhibited the same pattern with stand age as nitrogen in blueberry, but no consistent pattern in bunchberry. The relatively high concentration of nitrogen in the plants from the understory of the forests is similar to that in plants that appear to be light- or water-stressed (Rhoades 1979; Cates and others 1983, White 1984, Waring and others 1985).

The lack of between-stand differences in IVDMD was unexpected and is difficult to explain. The role of phenolics in dry-matter digestion is not well understood, but it appears that they tend to decrease *in vivo* digestibility of neutral detergent solubles (Mould and Robbins 1982). In

our samples, the greater concentrations of phenolics in the leaves from the clearcuts may have been offset by the correspondingly greater concentrations of nonstructural carbohydrates that should be readily digestible.

Detergent analysis and IVDMD of the Douglas Island samples (table 2) indicated no apparent differences in fiber composition or dry-matter digestibility of bunchberry between the forest and the clearcut. Blueberry, however, appeared to have slightly higher concentrations of fiber and correspondingly lower levels of dry-matter digestibility in the leaves from the forest than in those from the clearcut. This difference in digestibility appears contrary to the results from the Kennel Creek study area but is based on a much smaller sample. The July 26-28 IVDMD values from Kennel Creek (table 1) compare favorably with the August 3 IVDMD values reported

Table 2.--Detergent fiber composition, *in vitro* dry-matter digestibility (IVDMD), crude protein, and estimated digestible protein of *Vaccinium alaskensis* and *Cornus canadensis* leaves collected from an 8-year-old unburned clearcut and adjacent old-growth forest in July at the Douglas Island study area. All values are percentage dry weight

----- <u>V. alaskensis</u> -----		----- <u>C. canadensis</u> -----		
<u>Variable</u>	<u>Forest</u>	<u>Clearcut</u>	<u>Forest</u>	<u>Clearcut</u>
NDF ¹	41.5	35.1	23.0	24.4
ADF ²	25.2	20.0	16.5	17.4
Cellulose	13.3	8.7	13.3	14.1
Lignin/cutin	11.4	10.9	2.1	2.6
Residual ash	0.6	0.4	1.0	0.7
IVDMD	54.7	57.8	73.3	71.0
Crude protein	17.1	12.4	15.4	11.3
Digestible protein	11.2	4.8	7.5	3.8

¹NDF = neutral detergent fiber.

²ADF = acid detergent fiber.

by Hanley and McKendrick (1983) for Admiralty Island (45.8 percent for blueberry and 58.4 percent for bunchberry), though they are about 10 percentage points lower than the values for the July 5 samples from Douglas Island. The differences in IVDMD between the Kennel Creek and Douglas Island study areas probably reflect phenological differences in plant development. Regardless, the results from the Douglas Island samples (table 2) indicate that IVDMD was strongly related to fiber composition in both blueberry and bunchberry: estimates of apparent dry-matter digestibility based on fiber composition alone (equation for white-tailed deer, Mould and Robbins 1982) are 52.5 versus 55.5 percent and 79.1 versus 77.1 percent for forest versus clearcut in blueberry and bunchberry, respectively.

The differences in digestible protein concentration of the leaves from the clearcut versus the forest at the Douglas Island study area were especially pronounced (table 2). Both blueberry and bunchberry exhibited the common pattern of greater concentrations of crude protein in the forest than in the clearcut. But the combined effect of greater concentrations of crude protein along with lower concentrations of phenolics resulted in digestible protein concentrations 2.0 to 2.3 times greater in the forest leaves than the clearcut leaves for bunchberry and blueberry, respectively. These differences are especially significant in

relation to a crude protein requirement of about 12 percent for a lactating doe (8 percent digestible protein, assuming a protein digestion coefficient of 0.63-0.70) (Verme and Ullrey 1972; Holter and other 1979). Leaves from the forest would meet this requirement, but leaves from the clearcut would meet only about half the requirement.

It appears, therefore, that on a dry-weight basis, dry-matter digestibility (and, consequently, concentration of digestible energy) may not differ in leaves from forests and clearcuts, but the concentration of digestible nitrogen may be twice as great in leaves from forests than in those from clearcuts. Consequently, if deer are bulk-limited (dry-weight-limited) in the amount of food they can eat and process through their rumen, they would consume equivalent amounts of digestible energy but only about half as much digestible protein by feeding in an open clearcut compared to a forest, assuming all other factors equal.

On the other hand, the specific leaf weights of blueberry and bunchberry were, respectively, 2.0 and 2.3 times greater in the clearcut than the forest (0.006 vs. 0.003 g/cm² for blueberry and 0.007 vs. 0.003 g/cm² for bunchberry, Douglas Island study area). If dry-matter intake rates of foraging deer are largely a function of bite size (Wickstrom and others 1984), then intake rates should be greater in the clearcut than the

forest. Consequently, the rate of digestible energy intake would be greater in the clearcut than the forest and the rate of digestible protein intake in the clearcut may approach that in the forest. Thus, one of the critical questions is whether deer are more bulk-limited than time-limited in the amount and quality of food they can selectively harvest and process during the summer. We know that the two limitations are interrelated (Spalinger and others 1986) but do not know the precise nature of the interrelationships or which limitation is more important under a given set of environmental conditions.

In the palatability trials, all three deer distinguished between the blueberry leaves from the forest and those from the clearcut, and preferred (or at least ate more of) the leaves from the forest (fig. 1). One deer overwhelmingly preferred the leaves from the forest to those from the clearcut (4:1 ratio), while the preferences of the other two deer were less marked (ratios of 1.5:1 and 1.3:1). The pattern evident in figure 1 was consistent each of the 6 days of the feeding trial and was unaffected by switching feeding trays on the last day. The only exception was that on 1 of the days the female ate slightly more of the leaves from the clearcut than the forest. Forest leaves were preferred to clearcut leaves on all 17 of the other deer days.

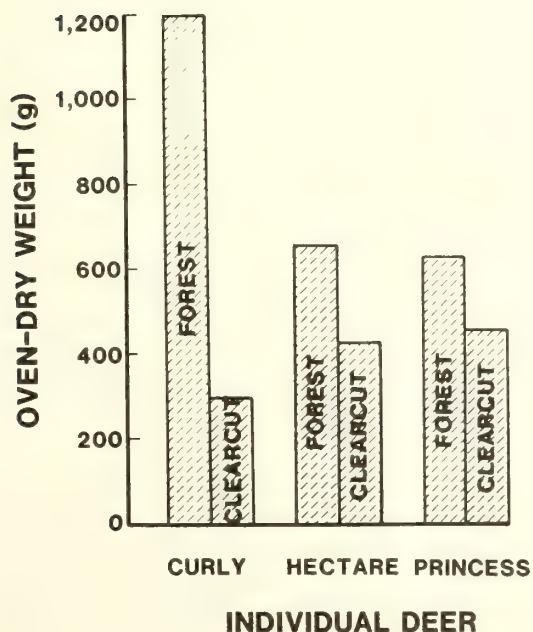


Figure 1.--Total consumption by three individual deer during a 6-day feeding trial of Vaccinium alaskensis leaves from an 8-year-old clearcut and adjacent old-growth forest at the Douglas Island study area.

CONCLUSIONS

Our current hypothesis is that blueberry and bunchberry plants growing in the shaded understories of forests in southeastern Alaska are essentially light-limited and allocate carbon primarily to growth and maintenance. On the other hand, blueberry and bunchberry plants growing in the open environments of young clearcuts appear to accumulate sufficient carbon for growth and maintenance as well as relatively high concentrations of carbon-rich secondary compounds such as tannins and other phenolics. We do not know whether high levels of these compounds are of use to the plant as ultraviolet light screens that transmit visible light (Lowry and others 1980), a means of tying up excess carbon, a deterrent to herbivores, or a combination of some or all of the above. In any case, plants in the open had higher concentrations of carbohydrates and phenolics and lower concentrations of nitrogen than did plants growing in the forest. The amount of solar radiation reaching the understory of forests in southeastern Alaska is typically less than 1 percent of that in the open (Alaback, unpublished data) and probably is the major environmental factor responsible for the observed differences in plant chemistry.

Our results indicate major environmentally controlled differences in forage quality for deer, with potential implications for deer productivity. Further research is needed to test the carbon/nutrient balance hypothesis under controlled conditions and to determine the relative importance of bulk- versus time-limitations for foraging deer.

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REFERENCES

- Alaback, P. B. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology*. 63: 1932-1948; 1982.
- Alaback, P. B. Unpublished data. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Juneau, AK.
- Billings, R. F.; Wheeler, N. C. The influence of timber harvest on yield and protein content of Vaccinium browse on three dominant soil types in southeast Alaska. In: Wallmo, O. C.; Schoen, J. W., eds. Sitka black-tailed deer: Proceedings of a conference; 1978 February 22-24; Juneau, AK. Ser. No. R10-48. Juneau, AK: U.S. Department of Agriculture, Forest Service, Alaska Region; 1979: 102-113.

- Bradford, M. M. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal. Biochem.* 72: 248-250; 1976.
- Brown, E. R. The black-tailed deer of western Washington. *Biol. Bull.* No. 13. Olympia, WA; Washington State Game Department; 1961. 124 p.
- Bryant, J. P.; Chapin, F. S., III; Klein, D. R. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*. 40: 357-368; 1983.
- Cates, R. G.; Redak, R.; Henderson, C. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. In: Hedin, P. A., ed. *Plant resistance to insects*. Washington, DC: American Chemical Society; 1983: 3-19.
- Cowan, I. McT. The ecological relationships of the food of the Columbian black-tailed deer, Odocoileus hemionus columbianus (Richardson), in the coast forest region of southern Vancouver Island, British Columbia. *Ecol. Monogr.* 15: 109-139; 1945.
- Einarsen, A. S. Management of black-tailed deer. *J. Wildl. Manage.* 10: 54-59; 1946a.
- Einarsen, A. S. Crude protein determinations of deer food as an applied management technique. *Trans. North Am. Wildl. Conf.* 11: 309-312; 1946b.
- Ellis, R. Concentration of minerals in Vaccinium parvifolium, a key species of browse for black-tailed deer. In: Meehan, W. R.; Merrell, T. R., Jr.; Hanley, T. A., eds. *Fish and wildlife relationships in old-growth forests: Proceedings of a symposium*; 1982 April 12-15; Juneau, AK. American Institute of Fishery Research Biologists; 1984: 397-402.
- Gates, B. R. Deer food production in certain seral stages of the coast forest. Vancouver: University of British Columbia; 1968. 105 p. Thesis.
- Goering, H. K.; Van Soest, P. J. Forage fiber analyses. *Agric. Handb.* 379. Washington, DC: U.S. Department of Agriculture, Agricultural Research Service; 1970. 20 p.
- Hanley, T. A. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. *J. Appl. Ecol.* 21: 423-436; 1984.
- Hanley, T. A.; McKendrick, J. D. Seasonal changes in chemical composition and nutritive value of native forages in a spruce-hemlock forest, southeastern Alaska. *Res. Pap. PNW-312*. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1983. 41 p.
- Hanley, T. A.; McKendrick, J. D. Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeastern Alaska. *J. Wildl. Manage.* 49: 103-114; 1985.
- Holter, J. B.; Hayes, H. H.; Smith, S. H. Protein requirement of yearling white-tailed deer. *J. Wildl. Manage.* 43: 872-879; 1979.
- Hultén, E. *Flora of Alaska and neighboring territories*. Stanford, CA: Stanford University Press; 1968. 1008 p.
- Isaac, R. A.; Johnson, W. C. Determination of total nitrogen in plant tissue, using a block digester. *J. Assoc. Off. Anal. Chem.* 59: 98-100; 1976.
- Jones, G. W. Influence of forest development on black-tailed deer winter range on Vancouver Island. In: Black, H. C., ed. *Proceedings of a symposium on wildlife and forest management in the Pacific Northwest*. 1973 Sept. 11-12; Corvallis, OR. Corvallis, OR: Oregon State University, Forest Research Laboratory, School of Forestry, 1974: 139-148.
- Klein, D. R. Range-related differences in growth of deer reflected in skeletal ratios. *J. Mammal.* 45: 226-235; 1964.
- Klein, D. R. Ecology of deer range in Alaska. *Ecol. Monogr.* 35: 259-284; 1965.
- Larsson, S.; Wirén, A.; Ludgren, L.; Ericsson, T. Effects of light and nutrient stress on leaf phenolic chemistry in Salix dasyclados and susceptibility to Galerucella lineola (Col., Chrysomelidae). *Oikos*. 43: [in press].
- Lowry, B.; Lee, D.; Hebant, C. The origin of land plants: a new look at an old problem. *Taxon.* 29: 183-187; 1980.
- Martin, J. S.; Martin M. M. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. *Oecologia (Berl.)*. 54: 205-211; 1982.
- McElroy, D. C. Secondary chemistry of sympatric plant species in an Atriplex-Artemisia grassland community. Albuquerque: University of New Mexico; 1984. 129 p. Thesis.
- Mould, E. D.; Robbins, C. T. Digestive capabilities in elk compared to white-tailed deer. *J. Wildl. Manage.* 46: 22-29; 1982.
- Rhoades, D. Evolution of plant chemical defense against herbivores. In: Rosenthal, G.; Janzen, D., eds. *Herbivores: their interaction with secondary metabolites*. New York, NY: Academic Press. 1979: 3-54.

- Robbins, C. T.; Hanley, T. A.; Hagerman, A. E.; Hjeljord, O.; Baker, D. L.; Schwartz, C. C.; Mautz, W. W. The role of soluble phenolics in defending plants against ruminants: protein digestion. *Ecology*. 68: [in press].
- Rochelle, J. A. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. Vancouver: University of British Columbia; 1980. 295 p. Ph.D. dissertation.
- Rose, C. L. Deer response to forest succession on Annette Island, Southeast Alaska. Fairbanks, AK: University of Alaska; 1982. 59 p. Thesis.
- Smith, D. Removing and analyzing total nonstructural carbohydrates from plant tissue. Research Report 41. Madison, WI: University of Wisconsin, Research Division, College of Agriculture and Life Sciences; 1969. 11 p.
- Smith, D. Addendum to Research Report 41: Removing and analyzing total nonstructural carbohydrates from plant tissue. Madison, WI: University of Wisconsin, Research Division, College of Agriculture and Life Sciences; 1979. 3 p.
- Sokal, R. R.; Rohlf, F. J. Biometry: the principles and practice of statistics in biological research. 2nd ed. San Francisco, CA: W. H. Freeman; 1981. 859 p.
- Spalinger, D. E.; Robbins, C. T.; Hanley, T. A. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. *Can. J. Zool.* 64: 312-321; 1986.
- Technicon Industrial Systems. Method No. 280-75A. Reducing sugars in tobacco extracts. Terrytown, NY: Technicon Industrial Systems; 1976.
- Van Horne, B. Demography of the longtail vole, Microtus longicaudus, in seral stages of coastal coniferous forest, southeast Alaska. *Can. J. Zool.* 60: 1690-1709; 1982.
- Verme, L. J.; Ullrey, D. E. Feeding and nutrition of deer. In: Church, D. C., ed. Digestive physiology and nutrition of ruminants. Vol. 3. Practical nutrition. Corvallis, OR: O & B Books; 1972: 275-291.
- Wallmo, O. C.; Schoen, J. W. Response of deer to secondary forest succession in southeast Alaska. *Forest Sci.* 26: 448-462; 1980.
- Waring, R. H.; McDonald, A. J. S.; Larsson, S.; Ericsson, T.; Wirén, A.; Arwidsson, E.; Ericsson, A.; Lohammar, T. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. *Oecologia (Berl.)*. 66: 157-160; 1985.
- White, T. C. R. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of Selidosema sauvis in a plantation of Pinus radiata in New Zealand. *Oecologia (Berl.)* 16: 279-301; 1974.
- Wickstrom, M. L.; Robbins, C. T.; Hanley, T. A.; Spalinger, D. E.; Parish, S. M. Food intake and foraging energetics of elk and mule deer. *J. Wildl. Manage.* 48: 1285-1301; 1984.

SECONDARY CHEMISTRY AMONG SYMPATRIC PLANT SPECIES

AND ITS RELATIONSHIP TO INSECT HERBIVORY

Rex G. Cates and Debra Carol McElroy

ABSTRACT: Leaves of 24 sympatric plant species in an Atriplex-Artemisia grassland community were analyzed for terpene, alkaloid, cyanide, and trypsin-precipitating content. Those species that were classified as unpredictable contained higher amounts of cyanide, myrtenal, citronellyl acetate, cinnamic acid methyl ester, and water in their leaf tissues than those in the predictable category. Leaves of those species classified as predictable were higher in alpha-pinene, an unidentified sesquiterpene, and in trypsin-precipitating capacity than those in the unpredictable category. Young leaves contained significantly higher concentrations of potentially toxic or defensive secondary metabolites than mature leaves. Usually, polyphagous herbivores preferred host plants in the predictable category that were devoid of the secondary metabolites analyzed; monophagous herbivores preferred predictable species. Polyphagous herbivores preferred mature leaves while monophagous herbivores preferred young leaves. When reared on young and mature leaves of Helianthus, larval and adult parameters of the polyphagous Estigmene were higher on the mature leaves.

INTRODUCTION

Much evidence indicates the importance of secondary metabolites in biological systems. These compounds are thought to be essential to the survival of plants, and represent foci in the mediation of interaction at the plant-plant, plant-herbivore, and plant-pathogen interfaces (Rosenthal and Janzen 1979; Green and Hedin 1986). They are recognized also as major factors in plant physiological and ecosystem processes.

However, no study has examined the distribution of secondary chemistry in a community of plant species and related this distribution to herbivory in that plant community. Janzen (1973) and Cates and Rhoades (1977) have discussed the community of secondary metabolites that might be expected in leaf tissue of sympatric plant species.

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Unpredictable or ephemeral species were suggested to be characterized by toxin or qualitative defensive chemistry (Feeny 1976; Rhoades and Cates 1976). Predictable species were suggested to converge on the digestibility-reducing or quantitative defensive systems. Escape in space and time was thought to be an effective mechanism in reducing herbivory especially against adapted herbivores. In general, adapted or more specialized herbivores were expected to prefer plant tissues or species that were typical of the unpredictable category while nonadapted or more generalized herbivores would prefer tissues and species that had converged upon quantitative defenses.

This paper is a synthesis of two major areas of research that we pursued from 1978 to 1984, and represents an attempt to relate the potential defensive chemistry of 24 sympatric plant species in an Atriplex-Artemisia grassland community to herbivore feeding patterns (Cates 1980, 1981; McElroy 1984; Cates and McElroy, submitted). Three classes of toxins and the trypsin-precipitating ability of leaf extracts of unpredictable and predictable plants were examined. First, we present the secondary chemistry of the plant species, and then the relationship of this chemistry to the young and mature leaves of the plant species. Finally, these data are discussed in terms of feeding patterns of monophagous-oligophagous and polyphagous herbivores.

MATERIALS AND METHODS

Site Location and Tissue Collection

The study site was located at the Petroglyph Open Space Preserve located 12 km northwest of the University of New Mexico campus, Albuquerque, NM. The site is a sandy area at the base of a volcanic escarpment; it supports a diverse plant community consisting predominantly of Artemisia filifolia, Atriplex canescens, Gutierrezia sarothrae, Dalea scoparia, and several desert annuals and grass species (table 1). This site previously had been characterized for plant density and herbivore plant and tissue preferences (Cates 1980, 1981; McElroy 1984). It has three semidistinct subsites: a sandy hill next to the escarpment, a less sandy flat area north and west of the hill, and an arroyo. The entire site measures approximately 300 m by 400 m.

Plant tissue was collected from April 1982 to September 1982. Plants were collected along random transects to ensure that the tissue obtained was representative of the species throughout the site. A minimum of 30 individual plants per species (except for Cucurbita of which there was only one individual on the site) were collected and their young or mature leaf tissues were pooled in three groups of at least 10 plants per group. This was done to minimize intraspecific chemistry variation due to genetic or microenvironmental differences among individual plants.

Young and mature leaf tissues for each species were collected separately just prior to flowering. This was done because it had been suggested that leaves present prior to and at flowering are of the most value to a plant, and therefore, would be highly protected (Krischik and Denno 1983). All plants of a particular species were collected at dawn within a 3-day period and immediately placed on ice. Whenever possible, the entire plant was uprooted. In the case of woody perennials, large branches were collected. The collected plants or branches were taken to McElroy's home (a few minutes from the site) where the leaves were picked by hand, separated according to their relative age, packaged in aluminum foil, and labeled. The packages were stored in an ultra-cold freezer (-80 °F) until the chemical analyses were performed.

Young leaves were located at a growing apex and were fully open but had not yet grown to average leaf size. Mature leaves were of average leaf size, were not located at a growing point, and did not show any signs of senescence. Leaves damaged by herbivory, pathogens, or abiotic influences were not collected.

Determination of Plant Species Predictability

The young and mature leaf tissues of 24 sympatric plant species were tested for toxins (terpenes, cyanogenic glycosides, and alkaloids), tannins (trypsin-complexing compounds) (table 1), and percent water content. The species investigated represented a predictability continuum from unpredictable short-lived annuals to dominant, highly predictable woody perennials. Plant species predictability (following Rhoades and Cates 1976) was used as the measure of the different resource types.

Predictability was defined as the availability of plant species as a food resource but did not include the capacity of the herbivores to locate their host plants. Predictability categories were determined by plant growth form (annual, herbaceous perennial, and woody perennial) and plant density data collected from 1978 through 1982 (McElroy 1984; Cates and McElroy, submitted). Herbaceous species having a density of less than 0.10 individual/m² for at least 7 months (one third of the density measurements) were classified as rare. Those species with densities greater than 1.0 individual/m² for at least 5 months were considered common, and herbaceous species with density measurements in between were considered to be of average abundance.

Variability of abundance was judged to be low if the range in density for the species did not exceed 1.0/m². Average variability was defined as a density range of 1.0 to 5.0/m², and high variability was considered to be a density range exceeding 5.0/m². Herbaceous species that were rare or exhibited a range of densities over the sampling years were defined as unpredictable. Woody perennial species were defined as predictable.

A total of 10 annual species representing eight families were included (table 1). Nine herbaceous perennial species from six families and five woody perennial species representing three plant families were sampled. Plant taxonomy was according to Martin and Hutchins (1980).

Greater description of the site, tissue collection, and detailed chemical methodology are found in McElroy (1984). Presented here are summaries of the chemical methods.

Water Content of Leaf Tissue

Leaf samples (1 g) were weighed on a Mettler H30 balance to within 0.1 mg. The samples were dried at 60 °C for 72 hours and reweighed. Percent water content was calculated as the ratio of weight lost to fresh tissue weight.

Alkaloid Analysis

Due to the diverse chemical nature of alkaloids, two methods were used to screen for their presence (Cates and McElroy, submitted). First, a modified Wall precipitation reaction (Cordell 1981) was used to determine if a plant produced alkaloids. Second, thin-layer chromatography was performed to determine the number of alkaloid compounds produced (McElroy 1984). Mayer's, Wagner's, Dragendorff's, and Ehrlich's reagents were used to detect alkaloids (including N-oxide alkaloids) in the above screening procedures. The thin-layer procedure also provided an estimate of the number of alkaloids present in a given tissue. In plants where alkaloids were present, high-pressure liquid chromatography (HPLC) was performed.

High-pressure liquid chromatography.--Those plants that gave positive precipitation reactions were subjected to analysis for specific types of alkaloids using high-pressure liquid chromatography. A modification of the method of Segall and Molyneux (1978) was used to test for the presence of pyrrolizidine alkaloids in Senecio longilobus. Using the method of Durbuc and others (1981) no steroidal alkaloids were found in any of the species.

Cyanogenic Glycoside Analysis

Leaf tissue samples were analyzed for the presence of cyanogenic glycosides as outlined by Mao and others (1965) using Conway microdiffusion glassware (Cates and McElroy, submitted). Color development was allowed to proceed at room temperature for 90 minutes after the addition of Chloramine T reagent, and the absorbance at 620 nm was read. The quantity of cyanide present was

Table 1.--Categories of plant species predictability and the associated secondary metabolites¹.

T = No. of terpenes, C = cyanide, A = No. of alkaloids, TP = trypsin-precipitating capacity,
M = mechanical (modified after Cates and McElroy, submitted)

Category	T	C	A	TP	M
<u>Unpredictable</u>					
<u>Annuals:</u>					
Boraginaceae					
<u>Cryptantha crassisejala</u>	-	-	-	-	+
Capparidaceae					
<u>Polanisia trachysperma</u>	2	+	-	-	-
Cruciferae					
<u>Dithyrea wislizenii</u>	-	+	-	-	-
Euphorbiaceae					
<u>Croton texensis</u>	21	-	-	-	-
Hydrophyllaceae					
<u>Nama dichotomum</u>	1	-	-	-	-
<u>Phacelia integrifolia</u>	+ ²	+	-	-	-
Loasaceae					
<u>Mentzelia laciniata</u>	-	-	-	-	+
<u>Herbaceous perennials:</u>					
Compositae					
<u>Senecio longilobus</u>	18	+	5	-	-
Cucurbitaceae					
<u>Cucurbita foetidissima</u>	-	-	3	-	+
Fabaceae					
<u>Astragalus lentiginosus</u>	-	+	-	-	-
<u>Dalea lanata</u>	16	+	1	-	-
<u>Hoffmanseggia jamesii</u>	-	-	-	-	-
Malvaceae					
<u>Sphaeralcea incana</u>	-	-	-	-	-
Polygonaceae					
<u>Rumex hymenosepalous</u>	-	-	-	-	-
Solanaceae					
<u>Solanum eleagnifolium</u>	-	-	-	-	+
<u>Predictable</u>					
<u>Annuals:</u>					
Chenopodiaceae					
<u>Salsola kali</u>	-	-	-	-	+
Compositae					
<u>Franseria acanthicarpa</u>	23	-	-	+	-
<u>Helianthus petiolaris</u>	16	-	2	-	-
<u>Herbaceous perennials:</u>					
Compositae					
<u>Machaeranthera canescens</u>	16	-	-	+	-
<u>Woody perennials:</u>					
Chenopodiaceae					
<u>Atriplex canescens</u>	-	-	-	-	+
Compositae					
<u>Artemisia filifolia</u>	27	+	2	-	-
<u>A. ludoviciana</u>	29	+	2	+	-
<u>Gutierrezia sarothrae</u>	30	+	1	-	-
Fabaceae					
<u>Dalea scoparia</u>	15	-	-	+	-

¹ + = secondary metabolites or mechanical properties present; - = secondary metabolites or mechanical properties not detected.

² Numerous unresolved terpenes.

determined by comparing the spectrophotometric reading obtained from a standard curve prepared from known amounts of potassium cyanide. Linear regression analysis was performed on the data and the linear function obtained was used to determine the concentration of HCN present in the leaf tissue.

Terpene Analysis

Leaf tissue was prepared for gas chromatographic analysis by weighing 300-mg leaf tissue to the nearest 1 mg. After extraction and filtering, 2 μ L aliquot of a concentrated ether extract was injected immediately into a Perkin Elmer Sigma 2B gas chromatograph equipped with a flame ionization detector and SE-54 fused quartz capillary column (15-m by 0.02-mm ID) from Hewlett Packard. The initial temperature of 70 °C was increased from the moment of injection at a rate of 6 °C per minute until the final temperature of 200 °C was reached. The temperature remained at 200 °C for 10 minutes.

Terpene peaks were recorded and integrated on a Hewlett Packard model 3390A integrator. The concentration of each peak was calculated relative to the concentration of the internal standard. The actual concentrations per sample for the internal standards were: fenchone 118.5 μ g, bornyl acetate 122.8 μ g, and fenchyl alcohol 118.8 μ g. Identification of the terpenes was achieved by comparing retention times of the terpene peaks to the retention times of known terpene standards, by spiking the peaks with standard terpene solutions, and by GC/MS on a Finnigan Quadrupole EICI instrument. The concentrations of all identified or numbered unknown terpenes were calculated to micrograms of terpene per gram dry weight of leaf tissue.

Determination of Protein-Complexing Compounds

Protein-complexing compounds (presumed to be hydrolyzable tannins) were analyzed using a modification of the method of Hagerman and Butler (1978) (McElroy 1984). To prevent oxidation of tannins, nitrogen gas was passed over the sample during the extraction and evaporation periods (Cates and McElroy, submitted). The absorbance of the supernatant, read at 595 nm, was compared to the standard curve of unprecipitated trypsin and converted to milligrams tannic acid equivalents per gram dry weight of leaf tissue.

Herbivore Feeding Preferences

The relationship between species predictability, secondary metabolites, and herbivory was examined. The methodology for sampling and determining leaf tissue and plant species preference is outlined in Cates (1980, 1981). For determining host plant preference, herbivores were visually sampled weekly during the 1977 through 1979 field seasons. A preference ranking that included the abundance of the plant species as well as the number of herbivores feeding on each plant species was calculated (Cates 1981).

Leaf tissue preference of each herbivore was determined by a relative tissue preference index that was based on the number of herbivores observed feeding on a plant and on the abundance of each leaf tissue type for each host plant (Cates 1980). At the same time the plant species abundances were determined, the plants were examined visually for leaf-chewing herbivores. Relative tissue preference (RTP) was calculated by dividing the number of feeding observations per tissue type per plant species by the amount of tissue available. The tissue with the highest value (the preferred tissue) was assigned a value of 100; the value for the less-preferred tissues was then normalized by dividing this number by the highest of the two and multiplying by 100.

To determine the effect of young and mature leaf tissues on larval growth rate, adult dry weight production, and egg mass production, larvae of Estigmene acraea (Arctiidae) were reared on leaf tissue of Helianthus petiolaris in a controlled environmental chamber. Fifty newly emerged, first-instar larvae were placed on either young (25 larvae) or mature (25 larvae) leaf tissues enclosed in glass petri dishes. Leaf tissue was replaced every 24 h to prevent drying and changes in the leaf tissue while the larvae were in the early instars, and every 12 h during the fifth and sixth instars. Larval growth rate was determined by subtracting the initial weight from the ending weight (pupal weight) and dividing this value by the number of days to reach pupation. As the female adults emerged, half were sacrificed to determine egg-mass production; the other half were sacrificed to determine adult dry weight production.

RESULTS

On the basis of the criteria used to determine the level of predictability of a given plant species, seven annuals in six families and eight herbaceous perennials in six families were designated as unpredictable (table 1). No woody perennials were deemed unpredictable resources. Predictable species included three annual species from two families, one herbaceous perennial (Compositae), and five woody perennials from three families. All annuals in the unpredictable category were short-lived and highly variable in abundance. This was epitomized by Cryptantha, Croton, and Nama. Most of the herbaceous perennials were relegated to this category because of their rarity. Rumex hymenosepalous emerged early in the spring (the end of February on occasion, but commonly around March 10-15) and completed flowering and seed production by the end of April or early May. Rumex is a species that generally escapes from herbivores at the study site due to its early emergence.

Three annuals were included in the predictable category because they were long-lived, often emerging in June and remaining in the community until September. None of the annuals in the unpredictable category were as long-lived. In terms of longevity, Machaeranthera appeared in late May and remained until October; during this

time individuals were continually producing new leaf tissue, flowering, and producing seed. Relative to the growing season, it behaved much like the woody perennials.

Much variation was found within and between predictability categories in the levels of the terpene, cyanide, alkaloid, and trypsin-precipitating secondary metabolites. Species in the unpredictable category averaged one class of compound in the leaf tissue (table 1). Exceptions were Senecio longilobus and Dalea lanata, both of which had three classes of compounds in their leaf tissues. Cryptantha, Nama, Mentzelia, Cucurbita, Astragalus, Hoffmanseggia, Sphaeralcea, Rumex, and Solanum (all assigned to the unpredictable category) were depauperate in the secondary chemicals analyzed. Of these, four were associated with potential mechanical defenses; one (Rumex) appears early in the growing season, and Nama is short-lived with little biomass per individual relative to the other species.

Species in the predictable group averaged 2.3 classes of compounds in their foliage, which is significantly different from the average of one in the unpredictable species ($p < 0.02$) (table 1). For terpenes, unpredictable species produced an average of 4.2 terpenes while predictable species produced 17.3 terpenes ($p < 0.01$). However, three unpredictable species (Croton, Senecio, and Dalea) produced 21, 18, and 16 individual terpenes, respectively.

To test the hypothesis that predictable species do not differ in qualitative or quantitative production of secondary metabolites relative to unpredictable species, stepwise discriminant analysis was performed (Neff and Marcus 1980; Dixon 1983). An eight-variable model was generated from the 77 variables incorporated in the analysis showing a significant difference between the two predictability categories (table 2). Figure 1 shows the separation of the predictability groups, with the species in the predictable category having a mean discriminant score of 1.52 and those in the unpredictable category having a discriminant mean of -0.98. The species in the predictable category were characterized by higher levels of tannic acid equivalents, alpha-pinene, and unknown sesquiterpene number 12 than the unpredictable category (table 2). The unpredictable category was higher in water, cyanide, myrtenal, citronellyl acetate, and cinnamic acid methyl ester content than the predictable category.

Table 3 delineates the species that produce unique toxin or qualitative secondary metabolites as defined by terpenes. The five species in the predictable category produced more unique compounds than did the three in the unpredictable category. Sesquiterpenes were important in the delineation of these categories.

To test for quantitative differences in secondary metabolites between young and mature leaves, a Wilcoxon signed rank analysis was done on the t values generated from t -tests that compared the mean concentrations of the compounds assayed in

the young and mature leaves for each species (Zar 1974). The 14 species that produced four or fewer secondary metabolites were not subjected to this analysis because a significant result could not be obtained due to limitations of the analysis (DeVore 1982; McElroy 1984). Of the 10 species tested, nine had significant t values, indicating significantly higher concentrations of secondary metabolites in young leaves than mature leaves (table 4).

Table 2.--Discriminant analysis for the classification of predictable and unpredictable species based on water and secondary metabolite content of leaves (d.f.=8, 129; $p < 0.0005$) (modified after Cates and McElroy, submitted)

Variable	Standardized coefficient
Percent water content	-0.4309
HCN	- .0036
Tannic acid equivalents	1.1461
Alpha-pinene	.0139
Myrtenal	- .1058
Citronellyl acetate	- .1945
Unknown sesquiterpene #12	.0678
Cinnamic acid methyl ester	- .2290

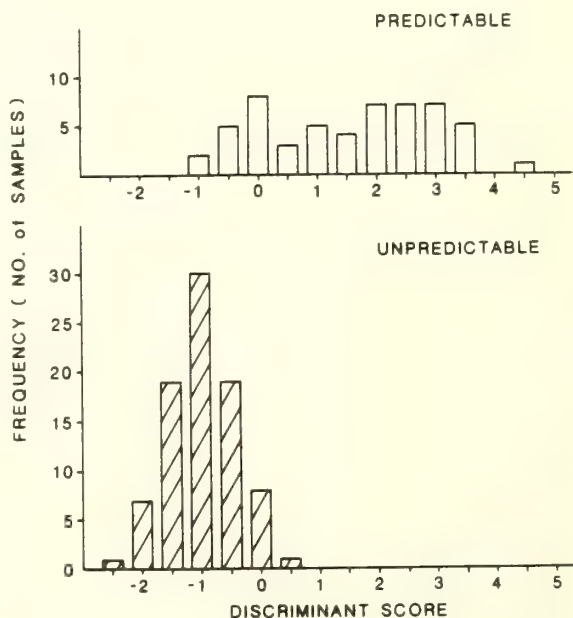


Figure 1.--Plot of the discriminant scores of leaf tissue samples of 23 species. Discriminant scores were calculated using an 8-chemical variable discriminant model.

Table 3.--Plant species producing unique toxin or qualitative secondary metabolites (after Cates and McElroy, submitted)

Species	P/U ¹	Compound
<u>Artemisia filifolia</u>	P	Unknown alcohol #1 Unknown sesquiterpene #21 Unknown sesquiterpene #22
<u>Artemisia ludoviciana</u>	P	Artemisia ketone Artemisia alcohol Sabinol Sabinyol acetate Sabinyol hydrate Thymol Unknown sesquiterpene #27 Unknown sesquiterpene #28
<u>Croton texensis</u>	U	Cinnamic acid methyl ester
<u>Dalea lanata</u>	U	Citronellal Citronellyl acetate Neryl acetate Unknown sesquiterpene #18 Unknown sesquiterpene #19 Unknown sesquiterpene #20
<u>Dalea scoparia</u>	P	Unknown sesquiterpene #26
<u>Franseria acanthicarpa</u>	P	Camphene hydrate Geraniol Beta-fenchene Beta-bisabolol Unknown sesquiterpene #13 Beta-farnesene Unknown sesquiterpene #16 Unknown sesquiterpene #17
<u>Gutierrezia sarothrae</u>	P	Trans-pinocarveol Alpha-camphene aldehyde Carvone Eucarvone Beta-eudesmol Unknown sesquiterpene #23 Unknown sesquiterpene #24 Unknown sesquiterpene #25 Verbenone Umbellulone Alpha-pinene oxide
<u>Senecio longilobus</u>	U	Unknown sesquiterpene #15 Alpha-farnesene

¹P = predictable resource, U = unpredictable resource.

Table 4.--Significant Willcoxon signed-rank statistics calculated on the t value comparing young and mature leaf tissues within each species. A negative sign on the z value indicates a higher concentration of potential toxin or qualitative chemistry in young leaves (after Cates and McElroy, submitted)

Species	Z-values	P
<u>Artemisia filifolia</u>	-4.144	0.0004
<u>A. ludoviciana</u>	-3.618	.0004
<u>Croton texensis</u>	-2.354	.0186
<u>Dalea lanata</u>	-2.025	.0440
<u>D. scoparia</u>	-2.959	.0031
<u>Franseria acanthicarpa</u>	-4.029	.0004
<u>Gutierrezia sarothrae</u>	-2.403	.0164
<u>Machaeranthera canescens</u>	-3.593	.0004
<u>Senecio longilobus</u>	-2.651	.0008

Of the six host plants observed fed on by the polyphagous lepidopteran Estigmene, Rumex was preferred in March and April, while Atriplex was preferred in July and August. Both species were devoid of the secondary metabolites that we analyzed (table 5). Senecio is an unpreferred host in March and April, but is second in preference in July and August. Hyles and Vanessa, both lepidopterans, prefer Rumex and Lupinus, respectively. (Lupinus was not present on the site the year secondary chemistry was measured.) Diapheromera, a walkingstick, preferred two predictable species (Atriplex and Dalea scoparia). The monophagous herbivores preferred Helianthus (a long-lived annual), Machaeranthera (a long-lived herbaceous perennial), and Artemisia filifolia (a woody perennial).

When comparing the feeding patterns of polyphagous and monophagous-oliophagous herbivores on young and mature leaf tissues, all three of the more generalized herbivores preferred mature leaf tissues of plants assigned to both predictability categories (table 6). Alternatively, both monophagous herbivores preferred young leaves of plant species of the predictable resource category.

Larvae of Estigmene, a lepidopteran with a host plant list of six species (Cates 1981), preferred mature leaves over young leaves of H. petiolaris (table 7). Larval growth rates, adult dry weight production, and egg mass production were significantly lower when larvae were reared on young leaves as compared to mature leaves.

CONCLUSIONS

Feeny (1976), Rhoades and Cates (1976), Cates and Rhoades (1977) and McKey (1979) hypothesized that ephemeral, unpredictable, young leaf tissues would be characterized primarily by low molecular weight toxin or qualitative defenses, and that predictable, mature leaf tissues would contain higher concentrations of digestibility-reducing or quantitative defenses. Patterns in the production

of secondary metabolites among the sympatric species at the Atriplex-Artemisia site support these ideas. The leaf tissues of the predictable species contained higher concentrations of trypsin-binding compounds and had higher concentrations of the higher molecular weight sesquiterpenes than the leaf tissues of the unpredictable species (tables 2 and 3). Alternatively, leaves of the unpredictable species did not contain tannins, but had higher concentrations of cyanide and the lower molecular weight terpenes than the predictable species (tables 2 and 3). Furthermore, young leaf tissues of 9 of the 10 species analyzed had higher concentrations of toxin or qualitative compounds than the mature leaves.

Cates and Rhoades (1977) predicted that selection by herbivores and pathogens would favor divergence in the production of toxins in leaf tissues of sympatric species, and convergence in the production of digestibility-reducing systems. This was supported by the terpenoid and trypsin-precipitating analyses. On the basis of terpenoids alone, eight of the species produced a total of 37 unique terpenes (table 3). Based on rf values, all of the alkaloids in the seven species that contained alkaloids were different. For example, in Senecio five pyrrolizidine alkaloids were identified (McElroy 1984). None of the other species contained this type of alkaloid, even though Cryptantha was a candidate for pyrrolizidine alkaloids since they are reported in the Boraginaceae.

Alternatively, all of the species producing trypsin-precipitating compounds were in the predictable category, and none of the unpredictable species were found to produce these compounds. However, only four of the nine species (44 percent) in the predictable category were shown to precipitate trypsin. A more rigorous test would be to measure binding capacity using a wide variety of proteins (such as hemoglobin, ribulose carboxylase, and proteins natural to the leaf tissues) since some secondary metabolites may not bind with trypsin but might with other proteins.

The question arises as to the accuracy, based on the secondary metabolites produced, of assigning plant species to the predictable and unpredictable categories based on growth form and abundance. Perhaps at other sites, some of the herbaceous perennials that were classified as unpredictable might be relegated to the predictable category. Several of the herbaceous perennials were classified as unpredictable species based on rarity at the site. Senecio and Dalea lanata reflect more of the predictable mode. These two species are characteristic of three of the five woody perennials in that they have at least three classes of compounds produced in the leaf tissues. In terms of the overall patterns, moving these two species to the predictable category would only enhance the differences already found in the distribution of toxins and digestibility-reducing secondary metabolites between the two categories. Based on rarity, Sphaeralcea is typical of other species in the unpredictable category. But this species is present during the entire growing season from June to October. In other communities Sphaeralcea may be abundant and more typical of the predictable category. However, no terpenoids, cyanide, alkaloids, or trypsin-precipitating compounds were found in its leaf tissues.

Several species were found to produce little if any of the secondary metabolites that were analyzed. The unpredictable species, Cryptantha, Nama, Mentzelia, Hoffmanseggia, Sphaeralcea, Rumex, and Solanum, and the predictable species, Salsola and Atriplex, may produce other compounds that were not analyzed in this study. For example, Atriplex may contain saponins (see McArthur, this proceedings). If species without any of the secondary metabolites we analyzed for were shown to contain other types of secondary metabolites, this would only increase the diversity of compounds, adding credence to the hypothesis that large chemical diversity exists among sympatric plant species. An obvious group to have included in this study is the monomeric phenolics.

Feeny (1976), Rhoades and Cates (1976), and Cates and Rhoades (1977) suggested that, in general, monophagous-olliophagous or adapted herbivores have evolved a preference for ephemeral or unpredictable species while polyphagous or less-adapted herbivores would prefer predictable or apparent species. Larvae of Estigmene, which is a polyphagous, bivoltine herbivore, preferred Rumex in the March and April sampling, and Atriplex in the July and August sampling (table 5). Both of these species were devoid of the secondary metabolites analyzed (table 1). In the July and August sampling, however, Senecio was important as a host plant in terms of the number of larvae feeding on it as was Atriplex (Cates 1981). Based on the three classes of secondary metabolites produced by Senecio (table 1), this would not be suspected; generally, the larvae selected other plants that were devoid of secondary metabolites (tables 1 and 5). However, it is known that alkaloids in Senecio decrease 40 to 60 percent when leaves begin to wilt. It may be that in July and August the defenses of Senecio are less effective resulting in its increased use as a host

plant. The feeding pattern of Estigmene appears to support the hypothesis that polyphagous or nonadapted herbivores prefer host plant tissues low in toxin defensive systems.

Hyles, Vanessa, and Diaperomera are less generalized in their diet (Cates 1981) but show a similar pattern to Estigmene; they prefer plants devoid of secondary metabolites (Rumex, Cryptantha, and Atriplex) (tables 1 and 5). Hyles and Vanessa at the species level have been shown to have large host plant lists. However, at the population level they appear less generalized in their diet than Estigmene (Cates 1981). Diaperomera prefers Dalea, which is known to have three classes of secondary metabolites, to Atriplex (table 5) but this may be due in part to its feeding on the young stem growth instead of leaf tissue. Analysis of young stem tissue may show it to be low in toxins and high in digestibility-reducing capacity.

The monophagous herbivores preferred predictable species: Helianthus which is a long-lived annual; Machaeranthera, an herbaceous perennial; and Artemisia filifolia, a woody perennial (table 5). These data are not supportive of the contention that specialists have evolved a preference for ephemeral and unpredictable species.

In every case, leaf tissue preferences of monophagous and polyphagous herbivores are consistent with the hypothesis that more specialized herbivores prefer ephemeral, unpredictable tissues, and generalized herbivores prefer the predictable, mature leaf tissues (table 6). For nonadapted herbivores, mature leaves are significantly preferred over ephemeral leaves, while adapted herbivores prefer significantly the young leaf tissues over the mature tissues. Young leaves are high in toxin or qualitative defenses while mature leaves are high in digestibility-reducing or quantitative defenses (tables 2 and 4, figure 1). Furthermore, it appears that young leaves of predictable species, as well as young leaves of some of the unpredictable species, are very diverse in terpenoid chemistry (table 3) adding to the contention that young leaves represent well the toxin mode of defense. Clearly, when Estigmene is reared on young or mature leaves, larval growth rate, adult biomass production, and egg mass production are greatest on the mature leaf tissues of Helianthus (table 7).

Growth rates were not measured for any of the plant species, so direct assessment of Bryant and others (1983) and Coley and others (1985) cannot be made. However, if we assume that predictable resources in general represent species with slower growth rates as compared to species in the unpredictable category, some preliminary comparisons can be made (Cates and McElroy, submitted). Predictable species are higher in carbon-based defenses than unpredictable species. Unpredictable species are higher in cyanide content than the predictable ones. However, six of the 15 (40 percent) and three of the 15 (20 percent) unpredictable resources produced

Table 5.--Plant species preferences of polyphagous and monophagous insect herbivores on annuals and herbaceous perennials (modified after Cates 1981)

Herbivore species	Plant species	Pref. ranking (PR)
Polyphagous herbivores:		
<u>Estigmene acraea</u> ¹	Chenopodiaceae ²	
	<u>Atriplex canescens</u>	2
	<u>Salsola kali</u>	1
	Compositae ²	
	<u>Gutierrezia sarothrae</u>	0
	<u>Senecio longilobus</u>	1
	Fabaceae ²	
	<u>Dalea scoparia</u>	1
	Polygonaceae ²	
	<u>Rumex hymenosepalus</u>	100
	Chenopodiaceae ³	
	<u>Atriplex canescens</u>	100
	<u>Salsola kali</u>	1
	Compositae ³	
	<u>Helianthus petiolaris</u>	5
	<u>Senecio longilobus</u>	84
	Fabaceae ³	
	<u>Dalea scoparia</u>	5
<u>Hyles lineata</u>	Polygonaceae	
	<u>Rumex hymenosepalus</u>	100
<u>Vanessa cardui</u>	Boraginaceae	
	<u>Cryptantha crassisejala</u>	1
	Fabaceae	
	<u>Lupinus pusillus</u>	100
<u>Diapheromera velii</u>	Chenopodiaceae	
	<u>Atriplex canescens</u>	79
	Fabaceae	
	<u>Dalea scoparia</u>	100
Monophagous herbivores:		
<u>Chlosyne lacinia</u>	Compositae	
	<u>Helianthus petiolaris</u>	100
<u>Stiria rugifrons</u>	Compositae	
	<u>Helianthus petiolaris</u>	100
<u>Chlosyne acastus</u>	Compositae	
	<u>Machaeranthera canescens</u>	100
<u>Hemileuca hera magnifica</u>	Compositae	
	<u>Artemisia filifolia</u>	100

¹Adults of Estigmene lay eggs twice/year.

²Eggs laid in March and April.

³Eggs laid in July and August.

Table 6.--Leaf tissue preferences of monophagous and polyphagous herbivores on annuals and herbaceous perennials (modified after Cates 1980)

Herbivore species	Plant species	Young	(N)	Mature	(N)
Polyphagous herbivores:					
<u>Estigmene acraea</u> ¹	Chenopodiaceae ²				
	<u>Atriplex canescens</u>	4	(5)	100	(71)
	<u>Salsola kali</u>	10	(3)	100	(34)
	Compositae ²				
	<u>Senecio longilobus</u>	0	(0)	100	(75)
	Fabaceae ²				
	<u>Dalea scoparia</u>	0	(0)	100	(26)
	Polygonaceae ²				
	<u>Rumex hymenosepalus</u>	10	(156)	100	(1984)
	Chenopodiaceae ²				
	<u>Atriplex canescens</u>	4	(5)	100	(69)
	Compositae ²				
	<u>Helianthus petiolaris</u>	0	(0)	100	(527)
	<u>Senecio longilobus</u>	19	(3)	100	(75)
	Fabaceae ²				
	<u>Dalea scoparia</u>	0	(0)	100	(26)
<u>Hyles lineata</u>	Polygonaceae				
	<u>Rumex hymenosepalus</u>	84	(11)	100	(123)
<u>Vanessa cardui</u>	Boraginaceae				
	<u>Cryptantha crassisejala</u>	0	(0)	100	(508)
	Fabaceae				
	<u>Lupinus pusillus</u>	0	(0)	100	(71)
Monophagous herbivores:					
<u>Chlosyne acastus</u>	Compositae				
	<u>Machaeranthera canescens</u>	100	(78)	0	(0)
<u>Hemileuca hera magnifica</u>	Compositae				
	<u>Artemisia filifolia</u>	100	(335)	0	(0)

¹Adults of Estigmene lay eggs twice/year.

²Eggs laid in March and April.

Table 7.--The effect of leaf tissue type of Helianthus petiolaris on the generalized Estigmene acraea.
Data are mean $\pm$ 1 SD

Parameters	Leaf tissue type	
	Young	Mature
Larval growth rate (mg)	17.6 $\pm$ 1.8	¹ 21.7 $\pm$ 4
Adult dry weight (mg)	61.0 $\pm$ 9.7	¹ 84.0 $\pm$ 18
Egg mass (dry wt)	61.0 $\pm$ 8.5	¹ 87.0 $\pm$ 20

¹p<0.003 for comparison of horizontal means.

cyanide and alkaloids, respectively, while three of the nine (33 percent) and four of the nine (44 percent) predictable species produced cyanide and alkaloids, respectively, indicating little difference if any in nitrogen-based secondary metabolites. Should *Senecio* and *Dalea lanata* be shifted to the predictable category, as the chemical evidence suggests, then the data do not support the growth rate hypothesis. If this were the case, then four of the 15 (27 percent) and one of the 15 (7 percent) of the unpredictable resources would produce cyanide and alkaloids, respectively, while five of the nine (57 percent) and six of the nine (67 percent) of the predictable species would produce cyanide and alkaloids, respectively. Furthermore, a greater diversity of terpenoids is found in the predictable species than the unpredictable ones (table 3). A knowledge of the availability and use of nutrients and moisture by the plant species would be useful in interpreting the patterns in the production of secondary metabolites.

The greater diversity of terpenoids in the predictable species suggests that biotic interactions such as those dealing with plants and herbivores, plants and pathogens, and plants versus plants are major influences in the production of secondary metabolites among sympatric plant species. Theories of the evolution of plant defenses must deal with variation in secondary metabolites among sympatric species having similar growth rates, since variation among and within sympatric plant species is now recognized as an important influence in the dynamics of herbivores (Denno and McClure 1983; Cates and Redak 1986).

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REFERENCES

- Bryant, J.; Chapin, F.; Klein, D. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*. 40: 357-368; 1983.
- Cates, R. G. Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. *Oecologia* (Berl.). 46: 22-31; 1980.
- Cates, R. G. Host plant predictability and the feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores. *Oecologia* (Berl.). 48: 319-326; 1981.
- Cates, R. G.; McElroy, D. C. H. Patterns in secondary metabolite production among sympatric plant species in an *Atriplex-Artemisia* grassland community. *Ecology* (submitted).
- Cates, Rex G.; Redak, R. Between-year population variation in resistance of Douglas-fir to the western spruce budworm. In: Green, M.; Hedin, P., eds. Natural resistance of plants to pests. Symposium Series 296, Washington, DC: American Chemical Society; 1986: 106-115.
- Cates, R. G.; Rhoades, D. F. Patterns in the production of antiherbivore chemical defenses in plant communities. *Biochemical Systematics and Ecology*. 5: 185-193; 1977.
- Coley, P.; Bryant, J.; Chapin, F. Resource availability and plant antiherbivore defense. *Science*. 230: 895-899; 1985.
- Cordell, G. A. Introduction to alkaloids: a biogenetic approach. New York: Wiley Interscience Publication, John Wiley and Sons; 1981. 1055 p.
- Denno, R.; McClure, M. Variable plants and herbivores in natural and managed systems. New York: Academic Press; 1983. 717 p.
- DeVore, J. L. Probability and statistics for engineering and the sciences. Monterey, CA: Brooks/Cole Publishing Co.; 1982. 640 p.
- Dixon, W. J. (chief ed.). BMDP statistical software, 1983 revised printing. Berkeley, CA: University of California Press; 1983. 733 p.
- Dubruc, C.; Caqueret, H.; Bianchetti, G. Determination of vincamine in human plasma using automated high-performance liquid chromatography. *Journal of Chromatography*. 204: 335-339; 1981.
- Feeny, Paul. Plant apparency and chemical defense. In: Mansell, R., ed. Recent advances in phytochemistry, Vol. 10. New York: Plenum Press; 1976: 1-40.
- Green, M.; Hedin, P., eds. Natural resistance of plants to pests. American Chemical Society; Symposium Series No. 296. Washington, DC: 1986. 243 p.
- Hagerman, A. E.; Butler, L. G. Protein precipitation method for the quantitative determination of tannins. *Journal of Agriculture Food Chemistry*. 26(4): 809-812; 1978.
- Janzen, D. H. Community structure of secondary compounds in plants. *Pure and Applied Chemistry*. 34: 529-538; 1973.

- Kirschik, V.; Denno, R. F. Individual, population, and geographic patterns in plant defense. In: Denno, R. F.; McClure, M. S. eds. Variable plants and herbivores in natural and managed systems. New York: Academic Press; 1983: 461-512.
- Mao, C. H.; Blocher, J. P.; Anderson, L.; Smith, D. C. Cyanogenesis in Sorghum vulgare. I. An improved method for the isolation of dhurrin; physical properties of dhurrin. *Phytochemistry*. 4: 297-303, 1965.
- Martin, W. C.; Hutchins, C. R. A Flora of New Mexico. Braunschweig, W. Germany: J. Cramer-Verlag; 1980. 2 Vols. 2561 p.
- McElroy, D. Secondary chemistry of sympatric plant species in an Atriplex-Artemisia grassland community. Thesis. Albuquerque, NM: University of New Mexico; 1984. 129 p.
- McKey, D. The distribution of secondary compounds within plants. In: Rosenthal, G. A.; Janzen, D. H. eds. *Herbivores: their interaction with secondary plant metabolites*. New York: Academic Press; 1979: 56-133.
- Neff, N. A.; Marcus, L. F. A survey of multivariate methods of systematics. New York:[privately published]; 1980. 243 p.
- Rhoades, D. F.; Cates, R. G. Toward a general theory of plant antiherbivore chemistry. In: Wallace, J.; Mansell, R. eds. *Recent advances in phytochemistry*. Vol. 10. New York: Plenum Press; 1976: 3-54.
- Rosenthal, G. A.; Janzen, D. H., eds. *Herbivores: their interaction with secondary plant metabolites*. New York: Academic Press; 1979. 718 p.
- Segall, H. J.; Molyneux, R. J. Identification of pyrrolizidine alkaloids (Senecio longilobus). *Research Communications in Chemical Pathology and Pharmacology*. 19: 545-548; 1978.
- Zar, J. H. *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall; 1974. 620 p.

BETWEEN-SPECIES DIFFERENCES IN LEAF DEFENSES OF TROPICAL TREES

Phyllis D. Coley

ABSTRACT: Rates of herbivory and patterns of leaf defense are presented for light-demanding and shade-tolerant tree species growing in a lowland rainforest in Panama. More than 85 percent of the annual leaf damage is due to grazing by insects. There are over three orders of magnitude difference between species in the rates of herbivory on mature leaves. More than 70 percent of this variation can be statistically explained by measured defenses. Species with little herbivore damage have tough, fibrous leaves with low concentrations of nitrogen and water. Tannin levels are not significantly correlated with herbivory. Shade-tolerant species have higher levels of defense and suffer less herbivory than species that require light gaps for establishment. This may be due to differences in inherent growth rates between species, with slow-growing species being better defended. Evidence is also presented showing a correlation between leaf lifetime and type of defense. Comparisons of general patterns of herbivory and plant defense are made between temperate and tropical forests.

INTRODUCTION

In this paper, I present patterns of herbivory and plant defenses observed in a lowland tropical forest, in an attempt to explain why some species are better defended than others. Initially, I will describe various plant characteristics that make leaves palatable to herbivores, and then present evolutionary arguments for why we might see differences in both type and amount of defense.

TROPIC/TEMPERATE COMPARISONS

Research was carried out in a lowland tropical rainforest on Barro Colorado Island (BCI) in Panama. The site is administrated by the Republic of Panama and the Smithsonian Institution, and has been protected from poachers and tree cutters since the 1920's. Most of the forest is at least 200 years old (Foster and Brokaw 1982).

Climate

Several aspects of the climate and forest are noteworthy since they contrast sharply with many temperate systems. First, seasonality is much less

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dramatic on BCI (Croat 1978; Leigh and others 1982). Temperatures average 25 °C year round, with much of the variation being diurnal. Annual rainfall is high (250 cm/yr), but includes a distinct 4-month dry season. The dry season is clearly important in the annual rhythms of both plants and animals; however, only a few tree species are completely deciduous, and insect abundances remain relatively high (Wolda 1978). In northern systems that experience much greater seasonal severity, environmental constraints on evergreenness and insect life cycles may play a much more dominant role in plant/herbivore interactions.

Light

In contrast to many shrub-dominated areas in the Western United States, light may be the most limiting and variable resource in the forest on BCI. The canopy is 30 to 40 m tall, reducing light levels at the forest floor to only 1 to 5 percent of full sunlight (Chazdon and Fetcher 1984). In comparison, light levels in gaps created by fallen trees can be dramatically higher, although light gaps comprise only about 5 percent of the area, the increased light levels make them important areas of productivity (Hubbell and Foster in press). Smaller breaks in the canopy create light flecks which can be the major source of carbon gain for plants below (Bjorkman and others 1972; Pearcy and Calkin 1983).

Accompanying the wide range of light conditions at the forest floor is a continuum in shade tolerance among different tree species (Whitmore 1978; Denslow 1980; Hartshorn 1980; Brokaw 1985). At one extreme are species found only in light gaps that rely on rapid germination and establishment once a gap is formed. At the other extreme are highly shade-tolerant species, that can persist for many years in the understory.

Diversity

Another important feature of the forest on BCI relative to temperate communities is its high species diversity. Per hectare, there is an average of 60 tree species with greater than 20 cm d.b.h. (Leigh 1982). This diversity has several interesting implications for herbivory. First, one might predict that there would be fewer specialist herbivores than in a less diverse community. Although there are no data with which to test this, my personal observations suggest the contrary: most leaf damage on BCI is done by relatively specialized insects. Another consequence of

tropical forest diversity is that one cannot understand general defense patterns and effects on herbivory by studying the dominant few species in the community. There simply aren't a few dominant species. However, working in a diverse community helps avoid the problem that general patterns may simply be a consequence of phylogenetic constraints on the dominant species. If large numbers of unrelated species have converged on a particular set of effective defenses, this can be a strong argument for the effectiveness of those defenses.

Herbivores

In neotropical forests, the vast majority of leaf tissue is eaten by insect rather than vertebrate herbivores. On BCI, 85 percent of the leaf area eaten annually is consumed by insects (Leigh and Smythe 1978). Vertebrate herbivores, notably sloths, iguanas, howler monkeys, and tapirs are conspicuous, but consume relatively little leaf material. I would argue that in neotropical forests the major selective pressure for the evolution of plant defenses is, therefore, due to grazing by insects.

HERBIVORY AND DEFENSES

To document general community-wide patterns, I measured herbivory and defenses for 47 of the most common canopy tree species on BCI (Coley 1983). These species represented a range of shade tolerance, from species that were gap specialists to those that could tolerate deep shade. To facilitate measurements, I worked with saplings. All individuals were studied in gaps to control for environmental influences and the availability of herbivores.

Patterns of Herbivory

Patterns of herbivory were quantified as the rate of damage to mature leaves. Over 400 saplings and approximately 10,000 leaves were marked and rates of herbivory measured during 6-week periods in each of the early wet, late wet, and dry seasons (Coley 1983). I emphasize the importance of measuring herbivory as a rate: the percentage of leaf area removed per unit of time. Because leaf lifetimes for different species vary by orders of magnitude, leaves are available to herbivores for different amounts of time. Single measurements of the amount of standing crop damage would therefore be misleading.

Average rates of herbivory differed enormously between the 47 study species (fig. 1). The least susceptible species lost an average of 0.0003 percent of its leaf area per day compared to 0.85 percent for the most damaged species (Coley 1983). This is a difference among species of over three orders of magnitude, despite the fact that study individuals were growing as neighbors in the same microhabitat, and were susceptible to the same herbivores.

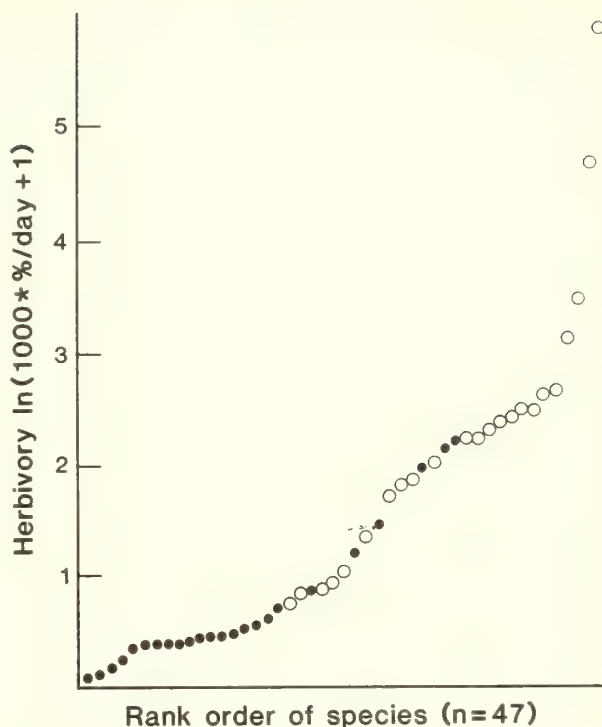


Figure 1.--Average annual rates of herbivory for mature leaves of 47 tree species on Barro Colorado Island, Panama. Herbivory measures are expressed as the natural log transformation of the percentage of leaf area consumed per day. Solid circles indicate shade-tolerant species, open circles indicate light-gap specialists.

Plant Defenses

Why are herbivores showing such strong preferences for certain species over others? To answer this, I measured leaf and plant properties that might influence rates of herbivory (Coley 1983) (table 1). Because it is impossible to measure all the secondary metabolites, I focused on a single widespread group: condensed tannins. There is considerable controversy surrounding the mode of action of tannins, but it is fairly well accepted that they serve some defensive function (Feeny 1970, 1976; Swain 1979; Bernays 1981; Martin and Martin 1982; Zucker 1983). I measured two forms of condensed tannins using the vanillin (VAN) and proanthocyanidin/BuOH (PRO) assays. Various components of fiber were also quantified (cellulose, acid-detergent fiber, neutral-detergent fiber, and lignin). Fiber provides structural support for the leaf, but it also reduces leaf digestibility for vertebrate and presumably invertebrate herbivores (Van Soest 1975; Milton 1979). Another measure related to fiber content is leaf toughness. This was measured as the amount of weight needed to punch a 3-mm rod through the leaf. Leaf pubescence was quantified as the density of hairs on the lower leaf surface. In addition to measuring potentially defensive properties, leaf nutritional value was estimated as the percentage of nitrogen and water.

Table 1.--Correlation coefficients for mature leaf characteristics and rates of herbivory for 47 canopy tree species on Barro Colorado Island, Panama. Values are the mean of several individuals for each species. Herbivory rates were measured throughout the year (Coley 1983)

Leaf characteristic	Correlation with herbivory
Tannin (VAN) % dw	-0.112
Tannin (PRO) % dw	-0.128
Fiber (NDF) % dw	-0.278 *
Fiber (ADF) % dw	-0.424 *
Lignin % dw	-0.223
Cellulose % dw	-0.473 *
Toughness (grams)	-0.515 *
Pubescence #/mm ²	0.635 *
Water %	0.507 *
Nitrogen % dw	0.287 *

* Significant at $P < 0.05$.

Table 1 correlates each leaf characteristic with herbivory. The magnitude of the correlation coefficient indicates the relative importance or effectiveness of each characteristic against herbivory. Water and nitrogen content were significantly positively correlated with herbivory. The various fiber components and the related toughness measure were all highly negatively correlated with herbivory. Tannin levels, however, showed no significant relationship to herbivory, and tannin/protein ratios were similarly uncorrelated. Pubescence was the only characteristic positively correlated with herbivory. This, along with its inverse relationship to other defenses, suggests that hairs may provide a simple way of identifying poorly defended species.

The results presented in table 1 show that species with tough, fibrous leaves of low nutritional value suffer the least amount of herbivory. Are these, however, the major leaf characteristics responsible for deterring herbivores? To examine this, I ran a multiple regression of herbivory as a function of the leaf characteristics mentioned above (Coley 1983). More than 70 percent of the variation in herbivory among species was statistically accounted for by differences in these leaf properties ($r = 0.84$, $p < 0.001$). This is an enormous amount of variation to explain for a natural system and suggests that nutritional and fiber contents are extremely important determinants of herbivory. Species not well defended by these measures are not escaping damage by other means (Rhoades and Cates 1976; Feeny 1976), but in fact are suffering high levels of herbivory.

BETWEEN-SPECIES DIFFERENCES IN DEFENSES

Defenses and Shade Tolerance

There is considerable variation among species in the extent of their defenses and in the resulting rates of herbivory. Are there any general defensive patterns, with certain groups of species tending to be better defended? For the species I studied on BCI, there were dramatic defensive differences related to the ability of each species to tolerate shade. In table 2, the 47 study species are divided into two categories based on their degree of shade tolerance. On average, species that were found only in light gaps were eaten six times more rapidly than shade-tolerant species. They had significantly lower concentrations of tannins, were less fibrous by all four measures, and only half as tough. In addition to being less well-defended, gap species had a higher nutritional value as measured by water and nitrogen contents.

Defenses and Growth Rate

The defensive differences between gap and shade-tolerant species (table 2) may be due to differences in inherent growth rates. Under the same microclimatic conditions, gap species grow more than twice as fast as shade-tolerant species (Coley 1983). Does the inherent growth rate of a species therefore show a relationship to the level of defense? For the 47 study species, there was a significant positive relationship between growth rate (annual height increase) and herbivory ($r = 0.52$, $p < 0.001$). This relationship was the same using other growth measurements such as annual leaf

Table 2.--Comparisons of mature leaf characteristics and rates of herbivory for 23 light-gap specialists and 24 shade-tolerant tree species on Barro Colorado Island, Panama. Values are the means for each species

Leaf characteristic	Light-gap specialist	Shade tolerant
Herbivory %/day	0.24	0.04 **
Tannin (VAN) % dw	0.8	2.4 *
Tannin (PRO) % dw	1.7	4.8 *
Fiber (NDF) % dw	41.3	51.1 *
Fiber (ADF) % dw	29.2	37.2 *
Lignin % dw	10.3	12.1
Cellulose % dw	17.4	23.4 *
Toughness (grams)	392	622 **
Water %	72	63 **
Nitrogen % dw	2.5	2.2 *

* significant at $P < 0.05$

** significant at $P < 0.01$

area production or maximum growth rate measured for an individual. There was also a significant negative relationship between growth rates and a linear combination of defenses ($r=0.72$, $p<0.001$). This indicated that the degree of investment in defenses was a function of inherent growth rate.

Conclusions

The general pattern that emerged from these data is that inherently slow-growing species show much higher investments in defense and consequently suffer much less herbivore damage. I and others argue that inherently slow growth rates select for high defense levels because the cost of defense is smaller and the impact of herbivory is potentially greater than for fast-growing species (Coley and others 1985; Gulmon and Mooney 1985). Inherent growth rates are determined evolutionarily by resource availability in the habitat to which a species is best adapted (Grime 1979; Chapin 1980). In my study, it was the shade-tolerant species that existed in resource-limited microhabitats and therefore had the slowest growth rates. Consequently they were also the best defended. This pattern of slow growers being better defended is also seen in areas where growth is limited by other resources such as water or nutrients (Brunig 1969; Janzen 1974; McKey and others 1978; Grime 1979; Bryant and Kuropat 1980; Bryant and others 1983; Coley and others 1985).

TYPE OF DEFENSE

The evidence presented above shows that slow-growing species tend to have greater amounts of defense, but makes no predictions concerning the type of defense. The diversity of plant secondary metabolites is enormous. Why are some species defended by tannins and others by alkaloids? What factors influence the type of chemical defense that will be used by different species? Part of the answer may be found by examining costs of different defenses under different conditions (McKey 1979, 1984; Coley and others 1985).

Traditionally, secondary compounds were considered inexpensive if they were present in low concentrations, and expensive if they occurred at high concentrations (Rhoades and Cates 1976; Feeny 1976). This ignores the potentially high cost associated with turnover (Coley and others 1985). Metabolically active compounds, such as alkaloids, cardiac glycosides, and mono- and di-terpenes can have half-lives on the order of hours or days (Robinson 1974; Waller and Nowacki 1978; Croteau and Johnson 1984). Although the pool size of these compounds is typically small, they have high rates of turnover. In other words, the plant must continually synthesize more compound to maintain the same concentration in the leaves. The cost of defense by these "mobile" compounds is therefore accumulated throughout the leaf life. This contrasts to "immobile" compounds such as fiber and tannins. There is an initial construction cost that can be high since they tend to be present in large concentrations. However, they are metabolically inactive, so there are essentially no

continued costs associated with turnover (Walker 1975; Swain 1979). Because of their metabolic inactivity, immobile compounds cannot be withdrawn from the leaf at senescence (McKey 1979). For leaves with short leaf life, the cost of defending with mobile defenses is likely to be less than the cost of immobile ones (McKey 1984; Coley and others 1985). As leaf life time increases, the costs of defense by immobile compounds are expected to be less.

The above predictions are supported by data I obtained on BCI. Leaf life times were measured on 46 species, and ranged from an average of 4 months to over 3 years (Coley 1981). There is a significant positive correlation between the condensed tannin content and average leaf life of each species ($r=0.46$, $p<0.005$). There is also a significant positive correlation between total fiber content and leaf life ($r=0.62$, $p<0.001$). This suggests that species with longer lived leaves have higher investments in immobile defenses.

The distribution of immobile defenses observed for the BCI trees is what would be predicted based on cost/benefit analyses. What other constraints besides costs could influence the advantage of one type of defense over the other? Are there conditions under which we would expect to find mobile defenses in long-lived mature leaves, and how might these vary between the temperate and tropical zones? Unfortunately there are few data with which to test this, particularly from the tropics. Studies of temperate trees have shown that insect damage or environmental stress can induce short-term production of several classes of secondary compounds (Haukioja and Niemela 1979; Baldwin and Shultz 1983; Rhoades 1985). Most often these seem to be mobile compounds such as simple phenols and monoterpenes. Their production, even in species with long-lived leaves, would be effective against temporary outbreaks of herbivores. Once the outbreak passed, the resources contained in the mobile defenses could be reallocated to other functions. The cost would therefore only be incurred for a short period. Hypothetically then, if short-term induction is a response to herbivory, and if insect outbreaks are more common in the temperate zone compared to the aseasonal tropics, one might expect induction of defenses to also be more common in the temperate zone.

Another condition that might favor mobile defenses in mature long-lived leaves is a strong seasonality of herbivore populations. Variation in the types and numbers of herbivores could make different defenses advantageous at different times of the year. Many temperate evergreen trees suffer primarily from insect herbivores in the summer and vertebrate grazers in the winter. This type of seasonality in herbivores is not generally as pronounced in the humid neotropics.

A final condition likely to favor mobile defenses is seasonality in nutrient availability. If nutrients are primarily taken up at a time of year when growth demands are low, they must be temporarily stored. Mobile defenses would be a good form of storage (Mooney and others 1983).

REFERENCES

- Baldwin, I. T.; Schultz, J. C. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221: 277-279; 1983.
- Bernays, E. A. Plant tannins and insect herbivores: an appraisal. *Ecological Entomology*. 6: 353-360; 1981.
- Brokaw, N. V. L. Gap-phase regeneration in a tropical forest. *Ecology*. 66: 682-687; 1985.
- Bjorkman, O.; Ludlow, M. M.; Morrow, P. A. Photosynthetic performance of two rainforest species in their native habitat and analysis of their gas exchange. *Carnegie Institution Yearbook*. 71: 94-102; 1972.
- Brunig, E. F. Forestry on tropical podzols and related soils. *Tropical Ecology*. 10: 45-58; 1969.
- Bryant, J. P.; Kuropat, P. J. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics*. 11: 261-285; 1980.
- Bryant, J. P.; Chapin, F. S. , III; Klein, D. R. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*. 40: 357-368; 1983.
- Chapin, F. S. , III. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*. 11: 223-260; 1980.
- Chazdon, R. L.; Fetcher, N. Light environments of tropical forests. In: Medina, E.; Mooney, H. A.; Vazquez-Yanes, C. eds. *Physiological ecology plants of the wet tropics*. Boston: Junk; 1984: 27-36.
- Coley, P. D. Ecological and evolutionary responses of tropical trees to herbivory: a quantitative analysis of grazing damage, plant defenses, and growth rates. Chicago, IL: University of Chicago; 1981. 151 p. Dissertation.
- Coley, P. D. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*. 53: 209-233; 1983.
- Coley, P. D.; Bryant, J. P.; Chapin, F. S. , III. Resource availability and plant anti-herbivore defense. *Science*. 230: 895-899; 1985.
- Croat, T. B. *Flora of Barro Colorado Island*. Stanford, CA: Stanford University Press; 1978. 943 p.
- Croteau, R.; Johnson, M. A. Biosynthesis of terpenoids in glandular trichomes. In: Rodriguez, E.; Healey, P. L.; Mehta, I. eds. *Biology and chemistry of plant trichomes*. New York: Plenum Press; 1984: 133-185.
- Denslow, J. S. Gap partitioning among tropical rain-forest trees. *Biotropica* (Supplement). 12: 47-55; 1980.
- Feeny, P. P. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*. 51: 565-581; 1970.
- Feeny, P. P. Plant apparency and chemical defense. In: Wallace, J.; Mansell, R. L. eds. *Biochemical interactions between plants and insects*. Recent Advances in Phytochemistry, vol. 10. New York: Plenum Press; 1976: 1-40.
- Foster, R. B.; Brokaw, N. V. L. Structure and history of the vegetation of Barro Colorado Island. In: Leigh, E. G.; Rand, A. S.; Windsor, D. M., eds. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington, DC: Smithsonian Institution Press; 1982: 67-81.
- Grime, J. P. *Plant strategies and vegetation processes*. New York: Wiley Press; 1979. 222 p.
- Gulmon, S. L.; Mooney, H. A. Costs of defense on plant productivity. In: Givnish, T. J. ed. *On the economy of plant form and function*. Cambridge, Great Britain: Cambridge University Press. 1985: 681-698.
- Hartshorn, G. S. Neotropical forest dynamics. *Biotropica* (Supplement). 12: 23-30; 1980.
- Haukioja, E.; Niemela, P. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. *Oecologia*. 39: 151-159; 1979.
- Hubbell, S. P.; Foster, R. B. Canopy gaps and the dynamics of a neotropical forest. In: Crawley, M. J. ed. *Plant ecology*. Oxford, Great Britain: Blackwell; in press.
- Janzen, D. H. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica*. 6: 69-103; 1974.
- Leigh, E. G., Jr. Why are there so many kinds of tropical trees? In: Leigh, E. G., Jr.; Rand, A. S.; Windsor, D. M. eds. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington, DC: Smithsonian Institution Press; 1982: 63-66.
- Leigh, E. G., Jr.; Rand, A. S.; Windsor, D. M. eds. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington, DC: Smithsonian Institution Press; 1982. 468 p.
- Leigh, E. G.; Smythe, N. Leaf production, leaf consumption and the regulation of folivory on Barro Colorado Island. In: Montgomery, G. G. ed. *The ecology of arboreal folivores*. Washington, DC: Smithsonian Institution Press; 1978: 33-50.

- Martin, J. S.; Martin, M. M. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins, and protein-precipitating constituents in mature foliage of six oak species. *Oecologia*. 54: 205-221; 1982.
- McKey, D. B. Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica*. 16: 81-99; 1984.
- McKey, D. B. The distribution of secondary compounds within plants. In: Rosenthal, G.; Janzen, D. eds. *Herbivores: their interaction with secondary plant constituents*. New York: Academic Press; 1979: 55-133.
- McKey, D. B.; Waterman, P. G.; Mbi, C. N.; Gartlan, J. S.; Strusaker, T. T. Phenolic content of vegetation in two African rain-forests: ecological implications. *Science*. 202: 61-64; 1978.
- Milton, K. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*. 114: 362-378; 1979.
- Mooney, H. A.; Gulmon, S. L.; Johnson, N. D. Physiological constraints on plant chemical defenses. In: Hedin, P. A. ed. *Plant resistance to insects*. Symposium Series 208. Washington, DC: American Chemical Society; 1983: 21-36.
- Pearcy, R. W.; Calkin, H. W. Carbon dioxide exchange of C3 and C4 tree species in the understory of a Hawaiian forest. *Oecologia*. 58: 26-32; 1983.
- Rhoades, D. F. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist*. 125: 205-238; 1985.
- Rhoades, D. F.; Cates, R. G. Toward a general theory of plant antiherbivore chemistry. In: Wallace, J.; Mansell, R. L. eds. *Biochemical interactions between plants and insects*. Recent advances in phytochemistry, vol 10. New York: Plenum Press; 1976: 168-213.
- Robinson, T. Metabolism and function of alkaloids in plants. *Science*. 184: 430-435; 1974.
- Swain, T. Tannins and lignins. In: Rosenthal, G. A.; Janzen, D. H. eds. *Herbivores: their interactions with secondary plant metabolites*. New York: Academic Press; 1979: 657-682.
- Van Soest, P. J. Physico-chemical aspects of fiber digestion. In: McDonald, I. W.; Warner, A. C. I. eds. *Proceedings of the fourth international symposium of ruminant physiology*; Armidale, New South Wales, Australia: University of New England Publishing Unit; 1975: 351-365.
- Walker, J. R. L. *The biology of plant phenolics*. New York: Crane, Russak and Company; 1975. 57 p.
- Waller, G. R.; Nowacki, E. K. *Alkaloid biology and metabolism*. New York: Plenum Press; 1978.
- Whitmore, T. C. Gaps in the forest canopy. In: Tomlinson, P. B.; Zimmerman, M. H. eds. *Tropical trees as living systems*. Cambridge, Great Britain: Cambridge University Press; 1978: 639-655.
- Wolda, H. Seasonal fluctuations in rainfall, food, and abundance of tropical insects. *Journal of Animal Ecology*. 47: 369-381; 1978.
- Zucker, W. V. Tannins: does structure determine function? An ecological perspective. *American Naturalist*. 121: 335-365; 1983.

Section 2. Palatability

PLANT SECONDARY METABOLITES AS FEEDING DETERRENTS TO VERTEBRATE HERBIVORES

P. Reichardt, T. Clausen and J. Bryant

ABSTRACT: The effects of specific phytochemicals on plant palatability to hares have been determined in feeding trials utilizing purified compounds in concert with quantification of deterrent substances in plant tissues having a range of palatabilities. These studies suggest that: plant chemical defenses rely on the properties of individual compounds, unpalatability is closely tied to exact molecular structure, and no broad class of secondary metabolites contains individual compounds with uniform deterrent properties.

INTRODUCTION

Limited understanding of the factors governing diet selection by herbivores has prompted numerous studies that demonstrate a relationship between an herbivore's feeding behavior toward some plant and certain physical or chemical properties of the plant. Palatabilities of plants have been claimed to be inversely related to levels of secondary metabolites (such as phenols, tannins, monoterpenes, and alkaloids) and physical properties (such as leaf toughness and twig diameter) and directly related to levels of nutrients (such as total carbohydrates and nitrogen). While data from various studies support such relationships, seldom do they support the assertion that the relationships are causative. While there are documented cases of plant unpalatability being correlated with total tannin content, we know of no case where it has been clearly demonstrated that tannin level is the governing factor leading to unpalatability. The purpose of this article is to present some conceptual and empirical approaches to critically testing the causative nature of the relationship between plant properties and palatability to herbivores.

Following the observations of Bryant and Kuropat (1980) that highly resinous plants and plant parts are generally associated with unpalat-

ability to boreal forest vertebrate herbivores, we are studying the role of secondary plant metabolites in diet selection by the snowshoe hare (*Lepus americanus*). While this study of snowshoe hare/woody plant interaction is important in its own right because of the impact of browsing by hares on boreal ecosystems (Cook and Robeson 1945; Bryant and Chapin, in press), we take this opportunity to present a more general discussion of phytochemical mediation of diet selection by a generalist herbivore.

In this context we will address two questions: How can the contention that phytochemicals play a role in diet selection by an herbivore be empirically substantiated? If diet selection is--at least in part--determined by phytochemicals, what can be said about the structure/activity relationships of phytochemicals?

Before exploring these questions, several points about unpalatable plants must be clarified. There must be some underlying reason for unpalatability (such as low nutrient status, undigestibility, toxicity, or simply bad taste). There must be some plant attribute that allows detection or recognition by an herbivore (such as morphology, color, taste, smell). Furthermore, these two attributes may or may not have their basis in a single plant property or substance (see for example Camazine 1985). These ideas are not new (Eisner and Grant 1981), but they are often forgotten.

The snowshoe hare is an excellent test animal for investigation of plant/vertebrate herbivore interactions. Hares are relatively abundant in the boreal forest; they can have a significant impact on their environment; and they show dramatic dietary preferences, both among plant species and among plant parts. Furthermore they can, with a bit of care, be maintained in captivity.

THE ROLE OF SECONDARY PLANT METABOLITES IN DIET SELECTION BY A VERTEBRATE HERBIVORE

Initially our work focused on developing empirical methods for investigating the hypothesis that secondary plant metabolites play a role in diet selection by the snowshoe hare. Palatability has been observed to be inversely proportional to resin (ether-extractables) content (Bryant 1981). Based on Bryant's observations that snowshoe hares generally avoid resinous plants (Bryant and Kuropat 1980) and that application of ether extracts of some boreal plants to either preferred

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browse or commercial food reduced their palatabilities (Bryant 1981), we chose to test this hypothesis utilizing *Betula* species. This genus includes species and growth stages that run the gamut from highly palatable to unpalatable.

It has been known for some time that hares find internodes of mature Alaska paper birch (*Betula papyrifera* var. *neoalaskana*) (Viereck and Little 1972) highly palatable, but that they reject juvenile internodes (Klein 1977) as well as buds and catkins of both growth stages (Bryant and Kuropat 1980). We were able to demonstrate very quickly that juvenile internodes of paper birch contained substantial quantities of a single substance that was essentially absent in mature internodes. Subsequent work revealed this substance to be a triterpene, papyriferic acid (Reichardt 1981), and that its addition to food offered to our colony of snowshoe hares reduced the food's palatability (Reichardt and others 1984).

Once we had identified a single substance that deterred hare feeding, our next step was to quantify levels of papyriferic acid in plant parts and correlate these levels both with palatability and deterrent potency. In a study designed to minimize the genetic variations between plants, we determined the levels of papyriferic acid in ramets of five highly palatable mature paper birch trees and in their respective unpalatable juvenile adventitious shoots. We found that papyriferic acid represented an astounding 11 percent of the dry weight of juvenile birch but less than 0.5 percent of the dry weight of genetically identical adults (Reichardt and others 1984). Palatability of paper birch to the snowshoe hare is directly related to levels of this single substance. We have come to accept this type of result--documentation of a deterrent substance and verification of its abundance in unpalatable plant material at active concentrations--as the minimum criteria needed to substantiate the claim of chemically mediated deterrence.

We have, however, carried out other types of experiments that provide alternative evidence that this substance deters hare feeding. In a study designed to probe the ecological effects of plant carbon/ nutrient balance (Bryant and others 1983a), we carried out a series of fertilization and shading experiments with a plot of sapling paper birches. Fertilization and shading allowed us to manipulate plant growth rate, and we found that both plant palatability and papyriferic acid levels were altered (fig. 1). The reasons behind these changes are beyond the scope of this paper (see Bryant and others, this proceedings), except to note that in the altered plants palatability consistently related to papyriferic acid levels in the expected manner while it did not consistently correlate with nutrient levels (such as nitrogen).

Another insight into a similar system was unexpectedly obtained in a 1984 field trip to the Kevo and Pakatti Gardens in northern Finland.

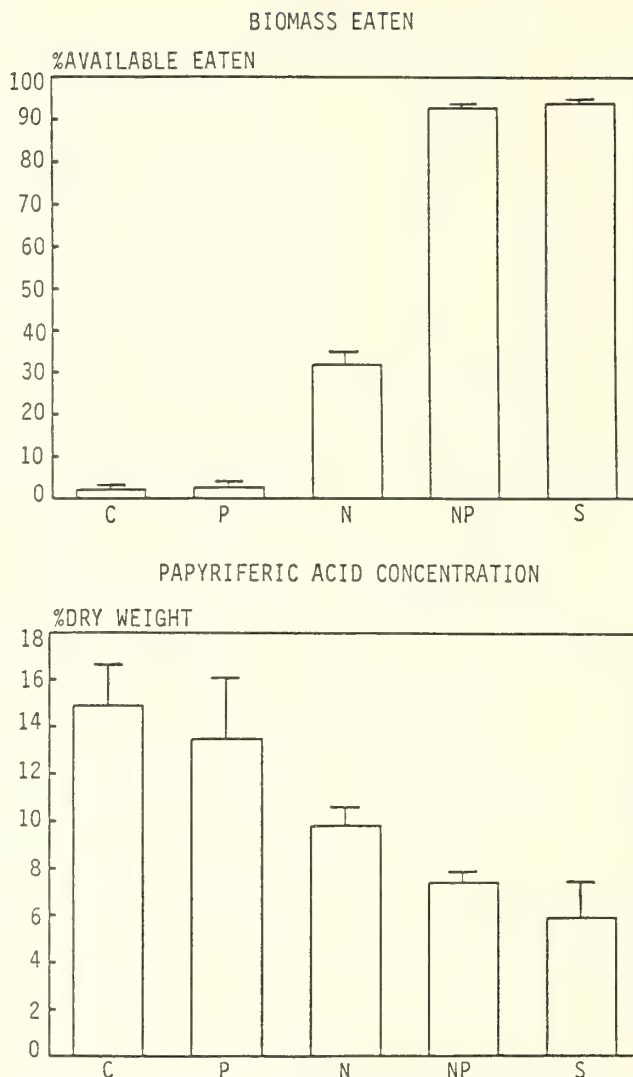


Figure 1.--Relationship between levels of papyriferic acid in *B. papyrifera* var. *neoalaskana* and palatability to snowshoe hares. Plant treatments are: control (C), nitrogen-fertilized (N), phosphorus-fertilized (P), nitrogen and phosphorus-fertilized (NP), and shaded (S). Standard errors are shown.

During the winter of 1982-83, mountain hares (*Lepus timidus*) broached the fences surrounding plots of birches maintained by Dr. Matti Sulkinoja of the University of Turku. Among the birches in these plots were *B. pendula* (a resinous, unpalatable birch), *B. pubescens* (a nonresinous, palatable birch), and some highly palatable hybrids of the two. Analyses of these plants (table 1) showed that browsing by mountain hares was inversely related to levels of papyriferic acid. However, more interesting is the apparent loss of chemical defense in the hybrid. Perhaps this signifies that birch's chemical defense against herbivores is a recessive trait held in a plant population only by browsing pressures.

All of these experiments dealt with the signaling aspect of plant palatability. We have not dealt with the other aspect of plant palatability--

underlying reasons--but we have initiated collaborative efforts with others who are beginning to investigate this aspect. Risenhoover and others (1985) demonstrated the ability of papyriferic acid to inhibit cellulose digestion in their in vitro assay with elk rumen fluid. Although these experiments may not be relevant to the hare studies, they do represent an empirical approach to investigations of the role that secondary plant metabolites can play in actually determining the food value of plants.

Table 1.--Relationships between level of papyriferic acid and palatability for three birch genotypes

Genotype	Papyriferic Acid (dry weight basis)	Plants Browsed in Kevo Garden	Plants Browsed in Pakatti Garden
	Percent	Percent	Percent
<u>Betula pubescens</u>	<0.06	10	8
<u>Betula pendula</u>	.8	2	2
<u>Betula pubescens</u> x <u>pendula</u>	<.04	30	50

MOLECULAR SPECIFICITY AND PALATABILITY

The literature of chemical ecology is full of reports of chemically mediated plant/herbivore interactions, but many of them focus on correlations of levels of certain classes of partially characterized substances (such as phenols, tannins, monoterpenes, alkaloids) with feeding behavior. Although there are good reasons to suspect that these classes of substances may have negative effects on plant palatability, the signals and underlying reasons for unpalatability must reside in discrete molecular interactions (Arnold and Hill 1972).

While the studies described in the previous section demonstrate empirical methods capable of documenting the roles secondary metabolites can play in plant palatability and suggest that these compounds can affect the food value of plants, they deal with a single substance and thus do not allow evaluation of the specificity of the relationship between structure and biological activity. Probing this question requires determining the palatabilities of a variety of phytochemicals present in browse or the palatabilities of structural analogues of nonpalatable substances. Our efforts have, to this point, concentrated on the first approach, although we have done a bit of work with analogues. Using the snowshoe hare as an herbivore, we have tested the effects of a variety of metabolites from Alaskan paper birch,

American green alder (Alnus crispa), and balsam poplar (Populus balsamifera) on palatability.

Even at this early stage of our investigations it is clear that a wide variety of structural types have negative effects on plant palatability to hares. The structures of several such phytochemicals are given in figure 2. In addition to papyriferic acid, we have found palatability-reducing phenols (pinosylvin), monoterpenes (cineol), sesquiterpenes (bisabolol), and one metabolite (6-hydroxycyclohexenone) that does not neatly fit into any of the standard biogenetic classifications. Thus we believe that the signaling aspect of plant chemical defense against the snowshoe hare relies on specific receptor-substrate interactions (Chapman and Blaney 1979) and not on physiochemical properties associated with general structural type.

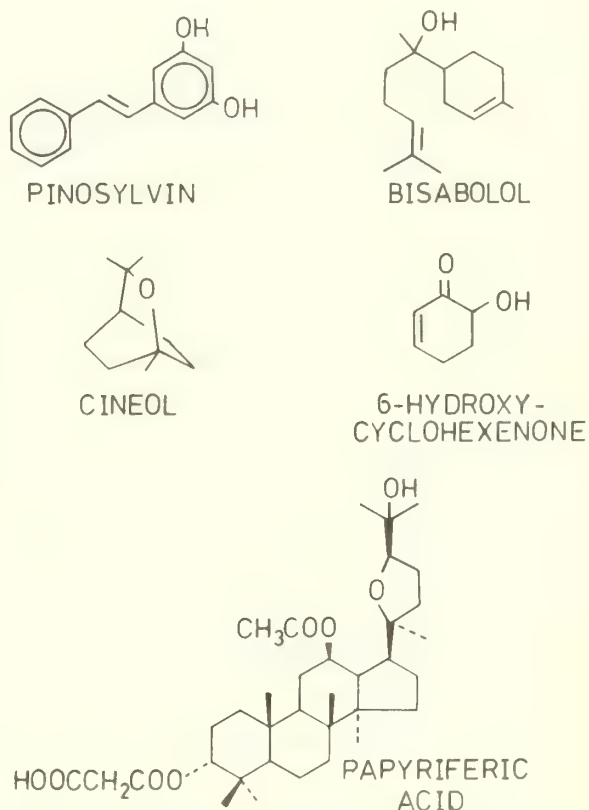


Figure 2.--Structures of several phytochemicals that deter feeding by snowshoe hares.

This idea is further substantiated by our discovery that no class of secondary plant metabolites contains uniformly active substances. Monoterpenes with widely varying potencies have been encountered (fig. 3), although we have yet to find a highly active monoterpene hydrocarbon. We have tested plant-derived phenols that vary in activity from highly deterrent to nearly benign (fig. 4), and we have preliminary evidence to indicate that the prototype--phenol itself--may even have attractive properties. In some cases, slight

structural modifications have little effect on deterrent potency while in others large differences are seen (fig. 5). In general one is left with the impression that the deterrent properties of a given substance are dependent on its detailed structure.

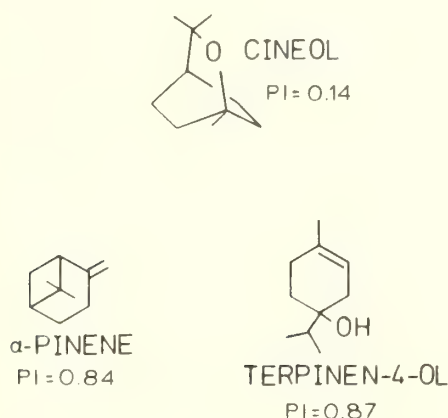


Figure 3.--Monoterpenes from *P. balsamifera* and their effects on feeding by snowshoe hares in bioassay experiments. Deterrent effects are given by preference index (PI) = percent treatment eaten $\div$ percent control eaten for compounds applied to food at 1.0 percent (dry weight basis).

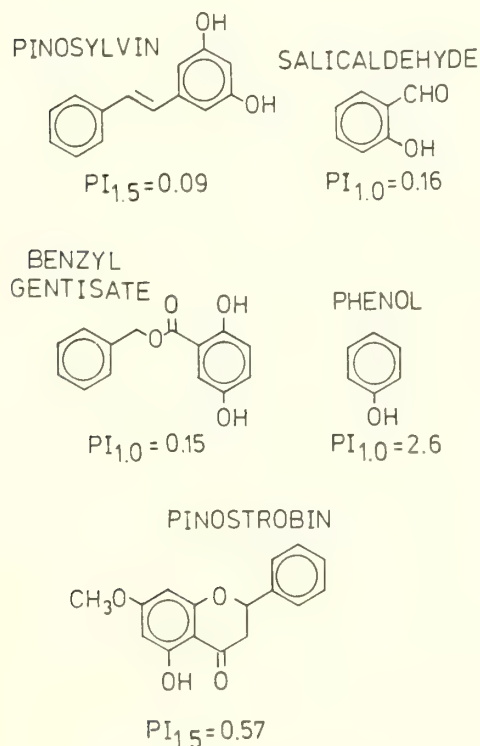
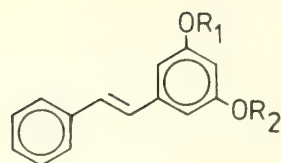


Figure 4.--Effects of selected phenols on feeding by snowshoe hares in bioassay experiments. Deterrent effects for samples applied to food at indicated percentages (dry weight basis) are given by preference index (PI) = percent treatment eaten $\div$ percent control eaten.



$\frac{R_1}{H}$	$\frac{R_2}{H}$	$\frac{PI}{0.09}$
H	H	0.09
H	CH ₃	0.12
CH ₃	CH ₃	0.63

Figure 5.--Relationship between structure of stilbene derivatives and effect on snowshoe hare feeding in bioassay experiments. Deterrent effects are given by preference index (PI) = percent treatment eaten $\div$ percent control eaten for compounds applied to food at 1.5 percent (dry weight basis).

Another interesting aspect of this specificity concerns the breadth of biological activity associated with a compound found to have activity in a single bioassay. In general it appears that a substance biologically active in one system (hare deterrence for example) has a broad spectrum of activity. Table 2 gives partial listings of biological properties ascribed in the literature to two compounds that we have found to function as deterrents to hare feeding. However, it is difficult to make strong arguments from data of this type because the reported biological activities of molecules are, in part, a function of how intensively they have been investigated.

Table 2.--Reported properties of two phytochemical defensive substances

Substance	Property	Reference
Pinosylvin methyl ether	feeding deterrent to hares	Bryant and others 1983b
	toxicity to mice	Frykholm 1945
	fungicidal	Lyr 1962
	bacteriocidal	Frykholm 1945
	insecticidal	Wolcott 1972
Bisabolol	feeding deterrent to mice	Henttonen and others in prep
	bacteriocidal	Dull and others 1956-57
	fungicidal	Szalunkai and others 1976
	insecticidal	Bar-Zeev 1980
	antiinflammatory agent	Jakovlev and others 1979
	toxicity to mammals	Habersang and others 1979
	ulcer inhibitor	Szelenyi and others 1979

Some of the compounds mentioned here have, to our knowledge, only been studied in our laboratory; our knowledge of them is limited due to experimental neglect. On the other hand bisabolol has been extensively investigated because of its occurrence in camomile, a plant used for medicinal purposes since antiquity. Nevertheless, it appears that nature's defense of plants relies on highly specialized molecules that are rather versatile in their roles as defensive agents.

CONCLUSIONS

Two hypotheses emerge from our studies at this point, and they both suggest productive lines for future experimentation.

Hypothesis 1: Nature operates on a molecular basis, and the ability of any phytochemical to serve as a defensive signaling substance requires only that the herbivore have a proper receptor.

Hypothesis 2: Molecular diversity is part of the chemical defense strategy of the plant kingdom against generalist herbivores, a situation suggesting toxin-based defenses.

Testing of hypothesis 1 requires more extensive investigation of structure/activity relationships of potential signaling substances utilizing both phytochemicals and synthetic analogues. A second, more exciting, area is that of signal/receptor interactions. Tests of hypothesis 2 must rely on extensions of in vitro studies like that of Risenhoover and others (1985) that can probe the differences between toxicity and digestion-inhibition. Although experimentally fraught with difficulty, such studies are crucial to our understanding of interactions between plants and generalist herbivores.

ACKNOWLEDGMENT

This work was supported by grants from the National Science Foundation (BSR-8207170 and BSR-8500160).

REFERENCES

- Arnold, G. W.; Hill, J. L. Chemical factors affecting selection of food plants by ruminants. In: Harborne, J. B., ed. *Phytochemical ecology*. New York: Academic Press; 1972: 72-102.
- Bar-Zeev, M. Studies of repellents against *Panstrongylus megistus* (Hemiptera: Reduviidae) in Brazil. *Journal of Medical Entomology*. 17(1): 70-74; 1980. *Chemical Abstracts* 92: 158922m; 1980.
- Bryant, J. P. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. *Science*. 213(4510): 889-890; 1981.
- Bryant, J. P.; Chapin, F. S., III. Browsing-woody plant interactions during boreal forest succession. In: Van Cleve, K., ed. *Taiga ecosystem function*. New York: Springer Verlag. [In press.]
- Bryant, J. P.; Chapin, F. S.; Klein, D. R. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*. 40(3): 357-368; 1983a.
- Bryant, J. P.; Kuropat, P. J. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics*. 11: 261-285; 1980.
- Bryant, J. P.; Wieland, G. D.; Reichardt, P. B.; Lewis, V. E.; McCarthy, M. C. Pinosylvins methyl ether deters snowshoe hare feeding on green alder. *Science*. 222(4627): 1023-1025; 1983b.
- Camazine, S. Olfactory aposematism: associated food toxicity with naturally occurring odor. *Journal of Chemical Ecology*. 11(9): 1289-1295; 1985.
- Chapman, R. F.; Blaney, W. M. How animals perceive secondary compounds. In: Rosenthal, G. A.; Janzen, D. H., eds. *Herbivores: their interaction with secondary plant metabolites*. New York: Academic Press; 1979: 161-198.
- Cook, D. G.; Robeson, S. B. Varying hare and forest succession. *Ecology*. 26(4): 406-410; 1945.
- Dull, G. G.; Fairley, J. L., Jr.; Gottshall, R. V.; Lucas, E. H. Antibacterial substances in seed plants active against tubercle bacilli. IV. The antibacterial sesquiterpenes of *Populus tacamahaca*. *Antibiotics Annual*. 1956-1957; 682-6; 1957.
- Eisner, T.; Grant, R. P. Toxicity, odor aversion, and "olfactory aposematism." *Science*. 213(4506): 476; 1981.
- Frykholm, K. O. Bacteriological studies of pinosylvine, its monomethyl and dimethyl ethers, and toxicological studies of pinosylvine. *Nature (London)*. 155(3937): 454-455; 1945.
- Habersang, S.; Leuschner, F.; Issac, O.; Thieme, K. Pharmacological studies of chamomile constituents. IV. Studies on the toxicity of (-)- α -bisabolol. *Planta Medica* 37(2): 115-123; 1979.
- Henttonen, H.; Bryant, J. P.; Clausen, T. P.; Reichardt, P. B. Effects of phytochemicals on feeding of microtine rodents. [In preparation.]
- Jakovlev, V.; Issac, O.; Thieme, K.; Kunde, R. Pharmacological investigations on the components of chamomile. II. New investigation on the antiinflammatory effects of (-)- α -bisabolol and bisabolol oxides. *Planta Medica*. 35(2): 125-140; 1979.

- Klein, D. R. Winter food preferences of snowshoe hares (Lepus americanus) in Alaska. Proceedings of The 13th international conference of game biology; 1977, Mar. 11-15, Atlanta, Ga. Washington, D.C.: Corporate Press; 1977: 266-275.
- Lyr, H. Detoxification of heartwood toxins and chlorophenols by higher fungi. Nature (London). 195(4838): 289; 1969.
- Reichardt, P. B. Papyriferic acid: a triterpenoid from Alaskan paper birch. Journal of Organic Chemistry. 46(22): 4576-4578; 1981.
- Reichardt, P. B.; Bryant, J. P.; Clausen, T. P.; Wieland, G. D. Defense of winter-dormant Alaska paper birch against snowshoe hares. Oecologia (Berlin). 65(1): 58-69; 1984.
- Risenhoover, K. L. Renecker, L. A.; Morgantini, L. E. Effects of secondary metabolites from balsam poplar and paper birch on cellulose digestion. Journal of Range Management. 38(4): 370-372; 1985.
- Szalonkai, M.; Verzar-Petri, G.; Florian, E. Data on the antifungal effect of the biologically active components of Matricaria chamomilla L. Acta Pharmaceutica Hungarica. 46(5-6): 232-247; 1976. Chemical Abstracts. 86: 101395p; 1977.
- Szelenyi, I.; Issac, O.; Thiemer, K. Pharmacological experiments with components of chamomile. III. Experimental animal studies of the ulcer-protective effect of chamomile. Planta Medica. 35(2): 218-227; 1979.
- Viereck, L. A.; Little, E. L., Jr. Alaska Trees and Shrubs. Agric. Handbook. 410. Washington, D. C.: USDA Forest Service; 1972: 134-136.
- Wolcott, G. N. Stilbene and comparable materials for dry-wood termite control. Journal of Economic Entomology. 46(2): 374-375; 1953.

CLASSIFYING AFRICAN SAVANNA TREES AND SHRUBS IN TERMS OF
THEIR PALATABILITY FOR BROWSING UNGULATES

Norman Owen-Smith and Susan M. Cooper

ABSTRACT: We studied food selection by hand-reared kudus, impalas, and domestic goats in savanna vegetation in South Africa. Woody plant species were assigned to four palatability classes: (1) palatable deciduous species favored throughout the year while in leaf; (2) relatively palatable evergreen species favored during the dry season; (3) unpalatable evergreen species, eaten only toward the end of the dry season; (4) unpalatable deciduous species, favored only when in new leaf if at all. Thorns or spines modified the acceptability of class 1 species. The primary factor discriminating palatable from unpalatable species was the condensed tannin content; crude protein levels were of secondary importance. Other nutrients, total polyphenols, fiber, alkaloids, cyanogenic compounds, and ether-soluble resins had little influence on acceptability.

INTRODUCTION

Some 65 percent of the African continent supports savanna vegetation, characterized by an association of trees or shrubs with a grass layer sufficiently well developed to sustain frequent fires. Rainfall is strongly seasonal, with a more or less regular alternation between wet and dry seasons. Two basic forms of savanna have been distinguished: arid/eutrophic savanna, typified by Acacia and other genera of the Mimosoideae; and mesic/dystrophic savanna, typified by genera such as Brachystegia and Burkea of the legume subfamily Caesalpinioideae (Huntley 1982). Acacia-dominated savanna is associated not only with low precipitation, but also with areas of 600-850 mm annual rainfall having clayey soils derived from volcanic or fine-grained sedimentary deposits. Brachystegia-dominated savanna (also referred to as miombo woodland) is typically associated with sandy leached soils of the central African plateau, underlaid by basement igneous rocks. Somewhat intermediate in their characteristics are combretaceous savannas, dominated by the genera Combretum and Terminalia, occurring on

sandy soils under moderate rainfall with less leaching.

Bell (1982) pointed out that regions with soils derived from basement igneous rocks carry a lower biomass of large herbivores for the same rainfall than regions underlaid by volcanic deposits or fine-grained sedimentary rocks. He suggested that low soil nutrient status promotes a high ratio of structural carbohydrates to metabolic constituents in grasses, and that woody plants in such areas are likely to contain high levels of secondary chemicals deterring herbivory.

Our observations were carried out at the study site of the South African Savanna Ecosystem Project (SASEP), located in the Nylsvley Nature Reserve in northern Transvaal. Prevailing soils are derived from Waterberg sandstone. Soils are sandy and low in available phosphorus (2 to 3 p/m) and cations, though not in nitrogen. Rainfall is moderate, averaging 630 mm annually, with some 85 percent falling during the summer months of October-March. The predominant vegetation is a savanna dominated by the tree species Burkea africana, with the multistemmed shrubs Ochna pulchra and Grewia flavescens dominating the understory. Also present are small 1 to 4 ha patches of Acacia-dominated vegetation, located on the sites of former human settlements. Here soils are locally enriched in phosphorus (10 to 30 p/m) and cations. Beyond the limits of the SASEP study area are more extensive areas of Acacia savanna on clayey soils along the flood plain margin of the Nyl River.

Our study was aimed at explaining the factors controlling the utilization of woody plant and forb species by browsing ungulates. Our specific objectives were to answer these questions:

1. What are the plant factors underlying variations in the utilization of different plant species?
2. How do different species of ungulate vary in their responses to these factors?
3. How do ungulates control their dietary intake from different vegetation components through the seasonal cycle?

A first step was to classify plant species in terms of the relative palatability of their foliage to browsing ungulates. Relationships between palatability and various chemical and physical factors could then be analyzed. In this report we summarize our findings on these

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questions; full details of results are published elsewhere (Owen-Smith and Cooper 1985, in press; Cooper and Owen-Smith 1985, 1986, University of the Witwatersrand in preparation).

METHODS

The animal species investigated included (a) greater kudu (*Tragelaphus strepsiceros*), a large, primarily browsing antelope; (b) impala (*Aepyceros melampus*), a medium-sized antelope known to be a mixed grazer-browser; (c) domestic "Boer" goats, also known for their mixed feeding habits. Wild populations of both kudu and impala occurred in the Nylsvley Nature Reserve and adjoining cattle ranches.

To enable close-range observations, young impalas and kudus were captured and bottle-reared. While in the rearing pen these animals were provided with cut branches from various woody species. They were also allowed into an adjoining 2-ha enclosure containing natural vegetation. Goats aged about 6 months were acquired from a nearby farm.

When aged 6 months the young impalas and kudus were released into a 213-ha enclosure in the study area, where they were allowed to range freely. The goats were observed in the same enclosure, but had to be locked overnight in a shed because of the presence of predators in the area.

Individuals of the three animal species were watched feeding at close range (1 to 5 m). To assess the relative acceptability of different plant species, we devised two measures for different observation conditions. During 1-hour observation sessions, the "Plant-based Acceptance" (PA) was defined as the proportion of available plants encountered during a foraging spell that the animal fed on. A plant was regarded as available if it was within neck reach of the animal's path of movement. The foraging pathway was marked with string and checked subsequently. For all-day observation sessions, the "Site-based Acceptance" (SA) was defined as the proportion of sites where a species was eaten in relation to the proportion of sites where that species was available. A woody species was regarded as available at a site if it was within readily visible range of the animal (within a radius of about 10 m of the foraging pathway). For practical convenience, each 30-minute foraging period was regarded as representing a separate site.

Supporting measurements of biting rates and bite sizes were made for particular plant species. Bite sizes were recorded by noting the number of leaves and length of stem ingested by the animal with each bite; samples of leaves of similar size were subsequently collected, dried, and weighed. Eating rates were calculated as the product of bite size and biting rate. Feeding times during daylight hours were determined from all-day observations.

Table 1.-- Plant species analyzed

Species and abbreviation	Family or subfamily	Growth form
<i>Acacia nilotica</i> (Acni)	Mimosoideae	tree
<i>Acacia tortilis</i> (Acto)	Mimosoideae	tree
<i>Burkea africana</i> (Buaf)	Caesalpinioideae	tree
<i>Combretum molle</i> (Como)	Combretaceae	tree
<i>Dichrostachys cinerea</i> (Dici)	Mimosoideae	shrub
<i>Dombeya rotundifolia</i> (Doro)	Sterculiaceae	tree
<i>Euclea natalensis</i> (Euna)	Ebeneaceae	shrub
<i>Grewia flavescens</i> (Grfl)	Tiliaceae	shrub
<i>Ochna pulchra</i> (Ocpu)	Ochnaceae	shrub
<i>Peltophorum africanum</i> (Peaf)	Caesalpinioideae	tree
<i>Rhus leptodictya</i> (Rhle)	Anacardiaceae	shrub
<i>Strychnos pungens</i> (Stpu)	Logoniaceae	tree
<i>Terminalia sericea</i> (Tese)	Combretaceae	tree
<i>Vitex rehmannii</i> (Vire)	Verbenaceae	tree

Fourteen common woody species, including both well-utilized and little-utilized plants, were chosen for chemical analysis (table 1). Composite samples of leaves were collected from 5 to 10 plants of each species in an adjacent unbrowsed enclosure. Samples were oven-dried at 60°C, and stored for subsequent analysis. The following quantitative chemical analyses were carried out: (1) crude protein, multiplying Kjeldahl nitrogen content by a factor of 6.25; (2) phosphorus, by reduction of phospho-molybdates to give a blue color; (3) potassium, calcium, magnesium, and sodium, by atomic-absorption spectroscopy; (4) fiber components, by the detergent method of Van Soest and Wine (1967); (5) total polyphenols, by the ferric ammonium citrate method (Jerumanis 1972; Daiber 1975); (6) condensed tannins, by the butanol-HCl method (Bate-Smith 1977; Swain 1979), using sorghum tannin as a standard; (7) ether-extract. Qualitative tests were carried out for alkaloids, cyanogenic glycosides, saponins, and terpenoids.

RESULTS

Palatability Classes

The woody species in the study area could be grouped into four fairly discrete palatability classes, considering seasonal variations in acceptability (fig. 1): (1) *Grewia flavescens*, *Vitex rehmannii*, *Combretum molle*, *Dichrostachys cinerea*, and *Acacia nilotica* were highly acceptable to the animals year-round, as long as they retained leaves; (2) *Acacia tortilis*, *Rhus leptodictya*, *Strychnos pungens*, and *Dombeya rotundifolia* became highly acceptable during the dry season, after class 1 species had started to shed their leaves; (3) *Euclea natalensis* was of low acceptability, except toward the end of the dry season when green foliage was generally in short supply; (4) *Burkea africana*, *Ochna pulchra*, *Terminalia sericea* and *Peltophorum africanum* were of low acceptability, except in the case of the first two species during the new leaf flush period.

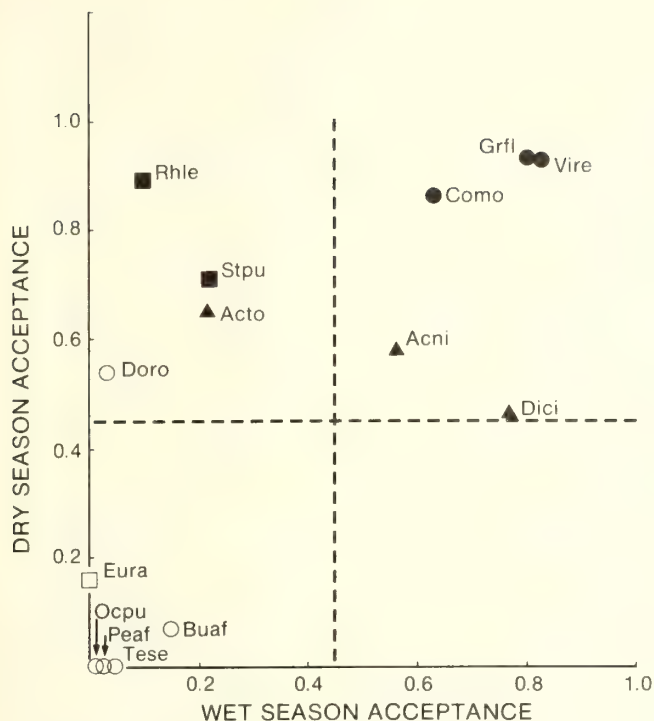


Figure 1.--Woody plant species ordinated in terms of their acceptabilities to kudus over the late wet season (December-April) and dry season (June-September) periods. For key to species abbreviations, see table 1.

For kudus category 1 included only deciduous species, including all except *Acacia tortilis* among spinescent species. Evergreen species were subdivided between categories 2 and 3. Category 4 species were all deciduous. The impalas differed by favoring both *A. tortilis* and *T. sericea* year-round. However, since the major portion of impala diet consisted of grass, *T. sericea* made up less than 1 percent of the food intake of the impalas. The goats showed a higher acceptance of *E. natalensis* and other evergreen species than did the two wild ungulate species, eating these species even during the wet season. This pattern was probably due largely to the fact that the goats foraged over a very limited area covering only about 10 ha around the shed where they were housed overnight. In consequence the foliage of more palatable species became depleted.

The impalas showed a relatively higher acceptance of spinescent species than did either the kudus or the goats. With their small mouths, impalas were adept at nibbling leaves from between thorns. The kudus at times ate shoot ends despite their thorns. The goats suffered a disadvantage from their floppy ears, which tended to become hooked on thorns. The reduced acceptability of certain spinescent species can be related to the restricting effects of thorns or spines, when coupled with small leaf size, on bite sizes. The effects of this restriction on eating rates were relatively greater for the larger kudus than for the smaller impalas and goats. Notably *Acacia tortilis* had the smallest leaves of any of the plants in the sample.

The impalas and goats included a considerable amount of leaf litter from deciduous species in their diets during the dry season. The kudus ate less leaf litter than the impalas and goats, due to the restricted eating rates obtained from the scattered leaves. Species with unpalatable foliage when intact were also rejected as leaf litter.

Nutrient Contents

There was no clear distinction between palatable and unpalatable species in terms of nutrient levels in leaves. However, all palatable species exhibited crude protein concentrations above 10 percent even in mature foliage. Some of the unpalatable species showed protein levels below this threshold. Correlations between acceptance and crude protein concentrations in leaves achieved statistical significance for kudus during the early growing season period, but not at other times of the year.

There was no distinction between phosphorus concentrations in the mature leaves of palatable and unpalatable species. However, certain of the unpalatable deciduous species showed markedly reduced phosphorus concentrations in their leaves (<0.5 mg/g dry mass) shortly before leaf abscission.

Fiber Components

There were no clear distinctions between palatable and unpalatable species in terms of fiber components. Nevertheless, the most fibrous species (ADF > 40 percent, ADL > 25 percent) was *Ochna pulchra*, one of the least unpalatable deciduous species. However, condensed tannins may be incorporated in the fiber fractions determined by detergent methods (Mould and Robbins 1981).

Polyphenols

There was no relation between total polyphenol contents and palatability. *Acacia nilotica*, which yielded polyphenol concentrations exceeding 25 percent (relative to a tannic acid standard) was a favored species. However, all five species showing condensed tannin (proanthocyanidin) contents exceeding 5 percent in mature leaves (relative to our sorghum tannin standard) fell into the unpalatable category. These included *Burkea africana*, *Dombeya rotundifolia*, *Ochna pulchra*, *Euclea natalensis*, and *Terminalia sericea*; but new leaves of the first three of these species were eaten despite their high condensed tannin levels.

Other Secondary Compounds

Alcoholic extracts of the leaves of *Burkea africana*, *Peltophorum africanum*, and *Terminalia sericea* foamed vigorously when shaken with water, suggesting the presence of saponins. Only *Strychnos pungen* and *Vitex rehmannii* gave a consistent reaction with Mayer's reagent, indicating the presence of alkaloids. Certain highly favored forbs gave even stronger reactions to tests for alkaloids.

Leaves of *Vitex rehmannii* had a strong odor suggesting a high content of monoterpenes, but this species was highly favored. None of the species in the sample responded positively to tests for cyanogenesis, and none had high contents of ether-soluble resins.

DISCUSSION AND CONCLUSIONS

Our findings suggest that unpalatability is associated mainly with high contents of condensed tannins. However, *Peltophorum africanum* was rejected by the animals despite a low condensed tannin content, indicating that other factors may be involved. Furthermore, new leaves of certain species were favored despite high condensed tannin concentrations. Notably, protein contents were also high in these young leaves. Discriminant function analysis separated palatable from unpalatable species on the basis of a canonical axis influenced positively by nitrogen and negatively by condensed tannin, with fiber having little further effect (fig. 2).

Zucker (1983) suggested that condensed tannins could benefit plants growing on nutrient-poor soils, by restricting rates of leaf decomposition and hence nutrient losses through leaching. In our study area those plant species prevalent on dystrophic soils all showed high leaf contents of condensed tannins. In contrast the species typical of the nutrient-enriched soils associated with former human dwelling sites were generally low in condensed tannins: although certain of these species showed high levels of total polyphenols (most notably *Acacia nilotica*).

Bryant and others (1983) suggested that deficiencies in soil nutrients promote the production of carbon-based secondary metabolites. Their hypothesis is that the carbohydrate excess is shunted into the shikimic acid pathway leading to polyphenol synthesis. In our sample of African savanna trees and shrubs, condensed

tannin contents in leaves are in accordance with this hypothesis. However total polyphenols show a conflicting pattern, and furthermore seem unrelated to palatability, at least to large herbivores. Zucker (1983) suggested that hydrolyzable tannins may function mainly as deterrents against insect herbivores. We noted outbreaks of defoliating caterpillars on *Burkea africana* and *Ochna pulchra*, indicating that high condensed tannin levels are not effective in preventing heavy foliage losses to insects. Possibly condensed tannins function mainly to restrict leaf degradation by microbes and fungi, with secondary effects on mammalian herbivores dependent on microbial fermentation.

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REFERENCES

- Bate-Smith, E. C. Astringent tannins of *Acer* species. *Phytochemistry*. 16: 1421-1426; 1977.
- Bell, R. H. V. The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley, B. J.; Walker, B. H., eds. *The ecology of tropical savannas*. Berlin, West Germany: Springer Verlag; 1982: 193-216.
- Bryant, J. P.; Chapin, F. S., III; Klein, D. R. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*. 40: 357-368; 1983.
- Cooper, S. M.; Owen-Smith, N. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia*. 67: 142-146; 1985.
- Cooper, S. M.; Owen-Smith, N. Effects of plant spinescence on large mammalian herbivores. *Oecologia*. 68: 446-455; 1986.
- Daiber, K. H. Enzyme inhibition by polyphenols of *Sorghum* grain and malt. *J. Sci. Food Agric*. 26: 1399-1411; 1975.
- Huntley, B. J. Southern African savannas. In: Huntley, B. J.; Walker, B. H., eds. *The ecology of tropical savannas*. Berlin, West Germany: Springer Verlag; 1982: 101-119.

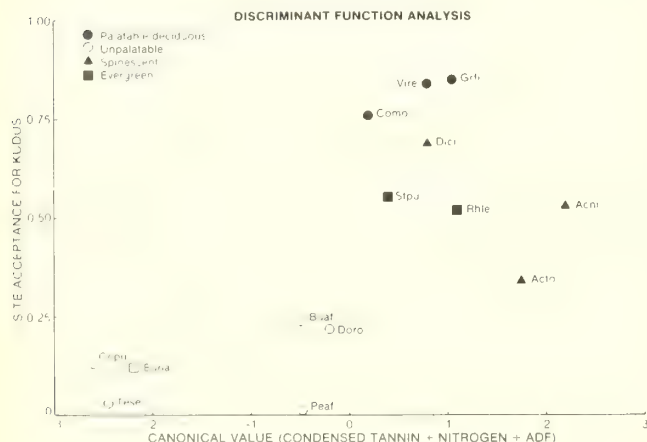


Figure 2.--Acceptance values of woody plant species for kudus, averaged over the complete year, plotted in relation to the first canonical axis discriminating the a priori classes of palatable and unpalatable species. For key to species abbreviations, see table 1.

- Jerumanis, J. Uber die veränderung der
polyphenole um verlauf des malzens und
maisshens. Brauwissenschaft 25: 313-322;
1972.
- Mould, E. D.; Robbins, C. T. Evaluation of
detergent analysis in estimating the
nutritional value of browse. J. Wildl.
Manage. 45: 937-947; 1981.
- Owen-Smith, N.; Cooper, S. M. Comparative
consumption of vegetation components by kudus,
impalas and goats in relation to their
commercial potential as browsers in savanna
regions. South African J. Sci. 81: 72-76;
1985.
- Owen-Smith, N.; Cooper, S. M. Palatability of
woody plants to browsing ruminants in a South
African savanna. Ecology; in press.
- Van Soest, P. J.; Wine, R. H. Use of
detergents in the analysis of fibrous feeds.
IV. Determination of plant cell-wall
constituents. J. Assoc. Off. Anal.
Chem. 50: 50-55; 1967.
- Zucker, W. V. Tannins: does structure determine
function? An ecological perspective. Am.
Nat. 121: 335-365; 1983.

STUDIES ON INTERACTIONS BETWEEN MOOSE AND TWO SPECIES OF BIRCH IN SWEDEN

A REVIEW

Kjell Danell and Roger Bergström

ABSTRACT: Two treelike birch species (*Betula pendula* and *B. pubescens*) constitute an important winter food for moose (*Alces alces*) in Sweden. Reviewed are here recent studies on: (1) moose browsing on these two species, (2) moose browsing on individual birches, (3) responses of birches to moose browsing, and (4) responses of moose to birches browsed previously.

INTRODUCTION

In Sweden there are three species of birch: *Betula nana* L., *B. pendula* Roth (= *verrucosa* Ehrh.), and *B. pubescens* Ehrh. (including *tortuosa* Ledeb.). (For a discussion of hybridization between the birches, see Danell and Ericson 1986). The first-mentioned species is a low-growing shrub, while the other two can form large trees. The two species *B. pendula* and *B. pubescens* are similar-looking and widely distributed throughout Sweden, but *B. pendula* becomes sparser in the mountain range and in the northernmost inland region close to the mountains (Hultén 1971). *Betula pendula* also generally has a higher growth rate (Fries 1964; Raulo 1977) and occurs in somewhat drier habitats (Arnborg 1946).

The birches are of medium preference as winter browse for moose, but due to their wide distribution and abundance in many habitats they form an important component of the moose diet (see review by Bergström and Hjeljord, in press). During winter twigs are browsed, but leaves as well as young shoots are taken during summer.

High moose densities in Sweden in recent years (Cederlund and Markgren, in press) focused interest on the interactions between moose and their browse plants, especially during winter. Here we review Swedish studies, as well as present unpublished research, on: (1) moose browsing on the two birch species, (2) moose browsing on individual birches, (3) responses of birches to moose browsing, and (4) responses of moose to birches previously browsed:

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MOOSE BROWSING ON THE TWO BIRCH SPECIES

Betula pendula and *B. pubescens*, closely related and similar in appearance, offer a good opportunity to study the underlying mechanisms governing food selection by moose.

Results of four browse surveys in central Sweden (59-62°N) show that the relative usage of *B. pendula* was 1.4-5.0 times higher than its relative availability (Danell and others 1985) (table 1). Higher usage of *B. pendula* than of *B. pubescens* was also found in another, but less quantitative, browse survey in central Sweden (59-60°N) by Stålfelt (1970).

Betula pendula and *B. pubescens* often grow in mixed stands, but the former is often more abundant in somewhat elevated and drier habitats. One possible explanation of the higher utilization of *B. pendula* is that moose for some reason, such as snow conditions, prefer these elevated habitats. To test whether the preference for *B. pendula* may be due to the habitat rather than to characteristics of the birch itself, we cut 2.5-3.0 m high birches of the two species in early winter and placed them side by side at test stations (Danell and others 1985). Fifty such stations were dispersed through a forest area of 140 km² in northern Sweden (64°N), where the two birch species were about equally abundant. After one winter's exposure, we estimated consumption of twigs from the test trees and found that 74-84 percent of the consumed twigs were from *B. pendula*.

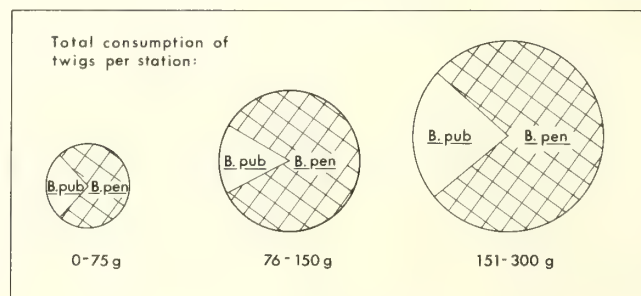


Figure 1.--Moose consumption of twig dry mass from *Betula pendula* (*B. pen*) and *B. pubescens* (*B. pub*) exposed at test stations within a 140-km² forest area in northern Sweden. Data from the 23 test stations visited by moose are divided into three groups according to the total consumption per station (after Danell and others 1985).

Table 1.--Availability and usage of *Betula pendula* shoots by moose reported for four browse surveys in central Sweden. The availability of *B. pendula* is expressed as the production of *B. pendula* over the total production of *B. pendula* and *B. pubescens*; the usage of *B. pendula* is expressed as the consumption of *B. pendula* over the total consumption of *B. pendula* and *B. pubescens* (after Danell and others 1985)

Locality	Geographic position	Size of area Km ²	Availability of <i>B. pendula</i>		Usage of <i>B. pendula</i>	
			-----	Percent	-----	-----
Furudal	61-62°N; 14-15°E	1 350	2		10	
Sunnäs	61°06'N; 17°05'E	6	66		94	
Grimsö ¹	59-60°N; 15-16°E	30	13		47	
Brommö	58°50'N; 13°40'E	15	34		87	

¹Unpublished information by A. Nyström.

(fig. 1). Approximately the same proportion of *B. pendula* was taken whether browsing pressure was low or high.

It is likely that the relative abundance of a birch species affects usage by moose. If moose have an instinct to mix various browse species in their diet, the rarest species will always be overutilized. *Betula pendula* was the rarest one in three of the four browse surveys (table 1). Therefore, we investigated 21 mixed birch stands in northern Sweden (63-65°N), where *B. pendula* cover ranged from 2 to 97 percent (Danell and Ericson 1986). In stands of 60 percent or less *B. pendula*, there was a preference for this species with regard to 1.5 to 3.0-m high trees (fig. 2).

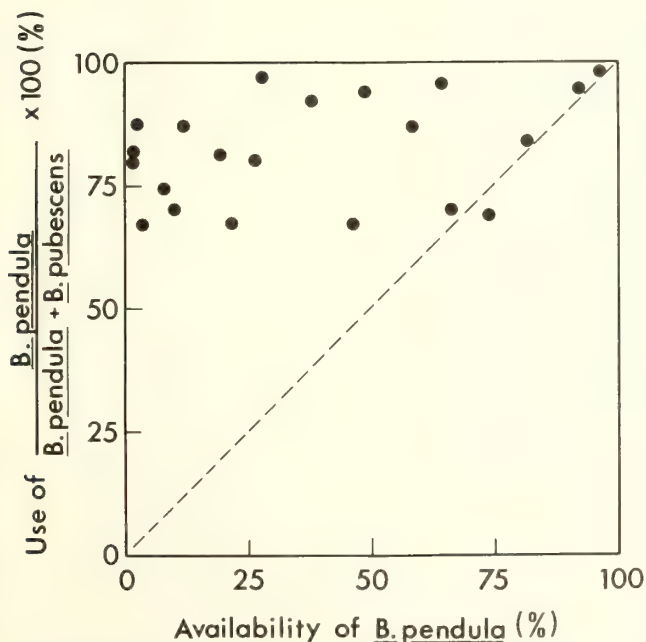


Figure 2.--Use (number of trees with more than 10 moose bites) by moose of *Betula pendula* in relation to the total use of *B. pendula* and *B. pubescens* in 21 mixed birch stands in northern Sweden with different availabilities (frequencies) of *B. pendula* (after Danell and Ericson 1986).

Birches of this height carry the largest amount of available browse for moose per tree. When comprising over 60 percent of a stand, *B. pendula* was still preferred but then its usage was close to availability. However, in all stands there were significantly more moose bites per tree on *B. pendula* than on *B. pubescens*. Thus, the preference for *B. pendula* seem to be more or less independent of its proportion in the stand.

The investigations reported here, which cover many localities in central and northern Sweden from around 59-65°N, indicate a common preference for *B. pendula*. From more northern areas the information is limited (table 2), but the same pattern prevails. Data from field surveys in southeastern Norway (59-61°N) also show that *B. pendula* is preferred to *B. pubescens* as a winter browse species (Rostad 1983).

However, some published data indicate differences in preference for *B. pendula*. Nyström (1980) found a reverse order of preference when studying selection and consumption of winter browse by four hand-reared moose calves that were introduced into a previously unbrowsed enclosure (5.42 ha) at Grimsö Research Station. On the other hand, unpublished data by A. Nyström from the forest area outside the fence show a preference for *B. pendula* (table 1). In inventories of moose damage in southern and central Sweden (56-60°N) (Westman 1958) and southern Finland (60-62°N) (Löyttyniemi and Piisilä 1983), no clear differences were found in damage to the two birches. The information reviewed here thus suggests that preference for *B. pendula* is strongest in northern Sweden and decreases with decreasing latitude. To test this hypothesis we analyzed data from a recent nationwide survey on damage in young forest stands (B.-Å. Näsund, unpublished observations). In the two birch height classes, 0 to 1.5 m and 1.6 to 3.0 m, there was a highly significant greater proportion of damaged *B. pendula* than of *B. pubescens* from the latitudes 64-67°N and 60-63°N (fig. 3). For 56-59°N there were only small differences in the frequency of damage. We do not yet know if this north-south pattern is consistent in critical field experiments.

Table 2.--Numbers of moose bites on 1.5- to 3.0-m high *Betula pendula* and *B. pubescens* at four locations in northern Sweden. The proportion of *B. pendula* in the birch stand (at least 700 birches determined to species) is given for each locality as well as the number of moose bites per tree on a random sample of 30 birch pairs (one specimen of each species; equal height; within <1.5 m from each other) (K. Danell, unpublished observations)

Locality	Geographic position	Proportion of <i>B. pendula</i>	Number of moose bites per tree		
			<i>B. pendula</i>	<i>B. pubescens</i>	Statistical test ¹
		Percent			
Kihlangi	67°41'N; 23°27'E	19	14.7±1.7	2.3±0.6	P < 0.001
Överkalix	66°14'N; 22°28'E	8	21.6±2.9	1.3±0.3	P < 0.001
Matojärvi	66°05'N; 23°44'E	57	48.3±3.3	5.9±1.0	P < 0.001
Gagsmark	65°07'N; 21°15'E	40	32.4±4.0	4.7±1.1	P < 0.001

¹Wilcoxon matched-pairs signed ranks test.

Besides this geographical effect on the relative preference between the birches, there is also an effect of tree height/age. Browsing on 1.0- to 1.5-m as well as on 1.5- to 3.0-m high birches was studied at four localities in northern Sweden (Dane11 and Ericson 1986). For both height

classes we found a preference for *B. pendula*, but the difference was less pronounced for the 1.0- to 1.5-m height class. When comparing smaller birches the preference order may be totally reversed, as indicated by data presented by Löyttyniemi and Rousi (1979) for a deciduous plantation in Finland. Further, we exposed 3-m high birches of the two species together with 3-m high tops of 6- to 9-m high trees to penned moose (Dane11 and others, in press). More twig biomass was taken from the tops of older trees (13 to 18 years) than from the younger (5 to 8 years) 3-m trees (fig. 4). There was a tendency for greater relative consumption of older *B. pendula* tops than younger trees.

To summarize, based on existing knowledge we find that 1.5- to 3.0-m high *B. pendula* are preferred to *B. pubescens* in large areas of northern and central Sweden. With decreasing latitude as well as decreasing tree height the difference in preference decreases or may even disappear. The

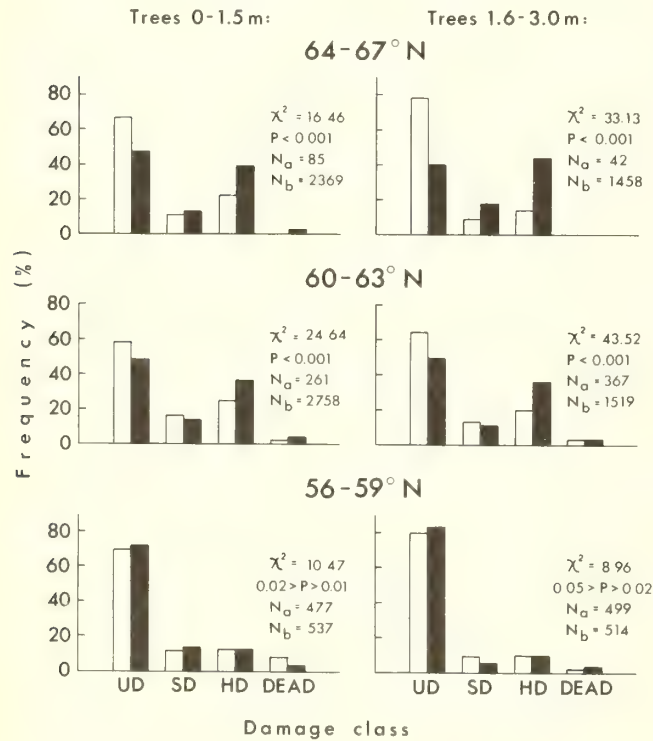


Figure 3.--Frequency distributions of *Betula pendula* (solid bars) and *B. pubescens* (open bars) stems classified according to the degree of moose damage during a survey of young forest stands in Sweden (B.-Å. Näslund, unpublished observations). UD = undamaged, SD = slightly damaged, and HD = heavily damaged. The sample size of *B. pendula* (N_a) and *B. pubescens* (N_b) is given for each case.

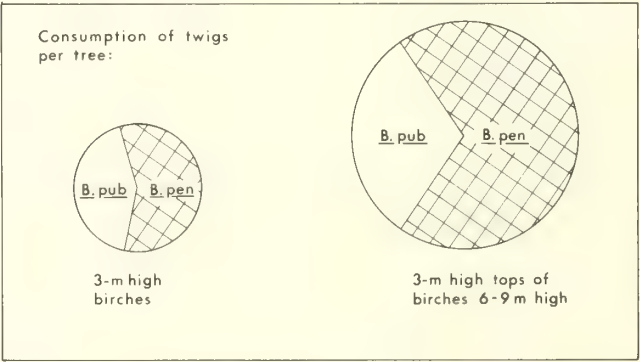


Figure 4.--Consumption of *Betula pendula* (*B. pen*) and *B. pubescens* (*B. pub*) by penned moose at Grimsö Research Station in Sweden. Cut 3-m high birches as well as 3-m high tops of birches 6 to 9 m high were "planted" in mixed stands inside the moose pen on February 10 1983 (after Dane11 and others, in press).

underlying mechanism that explains this food choice by moose is not yet known. For a discussion of inter- and intraspecific differences in morphology and chemistry of the two birch species refer to Danell and others (1985).

MOOSE BROWSING ON INDIVIDUAL BIRCHES

The spatial density of birches in a stand also affects moose browsing behavior. Vivås (in press) "planted" 2.5- to 3.5-m high *B. pubescens* at 10 different densities (0.04-0.4 birches per m²) on a mountain flank in central Norway. At the lowest birch densities, the mean number of moose bites per birch and mean bite diameter were larger than at higher birch densities. Consequently, the consumption of twig mass per birch was highest at low birch densities. However, the food intake per square meter of plot increased almost linearly with increasing birch density.

When moose browsed on 1.0 m high *B. pendula* during winter, 87 percent of the moose bites were taken at the height interval 0.5 to 1.0 m (fig. 5). With increased tree height (at least up to 2.5 m) a greater proportion of the bites were found in

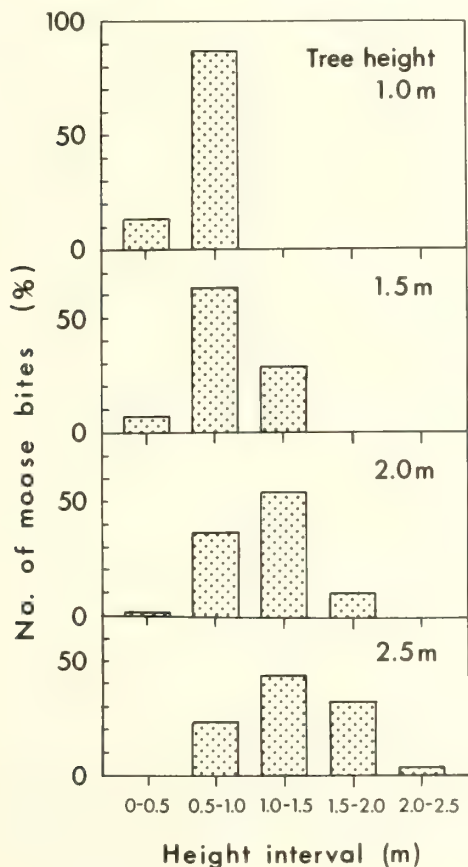


Figure 5.--The frequency distribution of moose bites at different height intervals of *B. pendula* (from 1.0 to 2.5 m high) exposed at 75 test stations inside the Sunnäs moose pen in central Sweden (R. Bergström, unpublished observations). The birches were available for moose from December 1, 1984, to January 25, 1985.

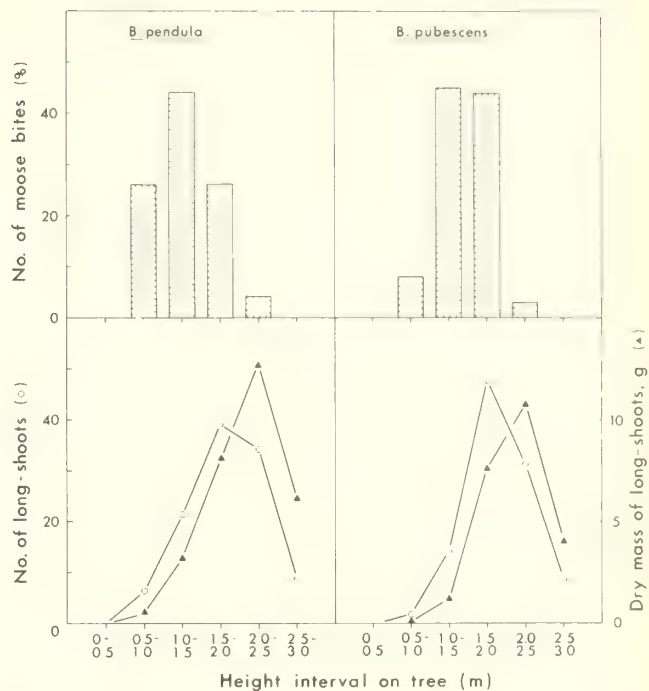


Figure 6.--The frequency distribution of moose bites on 2.5- to 3.0-m high birches as well as the distribution of long-shoots and their dry mass. The birches were exposed at test stations and visited by free-roaming moose in a forest area in northern Sweden from late October 1981 to late May 1982. For details see Danell and others 1985. (K. Danell, unpublished observations).

successively higher intervals. On 2.5-m birches, 72 percent of the bites were within the 1.0 to 2.0 m interval. Another field experiment with 2.5- to 3.0-m high *B. pendula* and *B. pubescens* showed that 70 and 89 percent of the moose bites, respectively, were taken from positions 1.0 to 2.0 m high on the birches (fig. 6). Distributions of moose bites on birches recorded during a field survey yielded a similar picture (Danell 1983). The frequency distributions of moose bites at various height levels are not directly related to the number or dry mass of long-shoots available at different height intervals (fig. 6). A more simple explanation is that browsing mainly at the 1.0- to 2.0-m level is the least energy-demanding behavior for moose. However, sometimes stems of birches are broken by the moose in order to reach twigs situated at higher positions. In the Sunnäs moose pen there was a general increase in the frequency of broken birch stems with increasing moose density (table 3). The preferred *B. pendula* generally had a higher frequency of stem breakage than *B. pubescens*. In small, individual birch stands it is, however, difficult to demonstrate that high browsing pressure always leads to a high frequency of stem breakage.

The mean diameter at the point of browsing on birches is commonly around 2 or 3 mm (Danell 1983; Rostad 1983; Vivås in press) (fig. 7). When the

Table 3.--Frequency of stembreakage by moose on *Betula pendula* and *B. pubescens* in the Sunnäs moose pen (6.2 km²) during an increase in the moose population. The frequencies recorded for the winters 1979-80 to 1983-84 are from forest stands with a mean age around 10 or 25 years in 1979 (R. Bergström, unpublished observations)

Stand	Frequency of stem breakage during the winters				
	1979-80	1980-81	1981-82	1982-83	1983-84
----- Percent -----					
10-year-old stands:					
<i>B. pendula</i>	0.7	2.0	7.1	11.0	13.1
<i>B. pubescens</i>	.0	.6	1.0	1.7	2.5
25-year-old stands:					
<i>B. pendula</i>	3.9	3.8	7.2	7.7	21.6
<i>B. pubescens</i>	.0	.0	.0	3.1	2.9
No. of moose per km ²	1.3	2.3	3.4	4.6	5.2

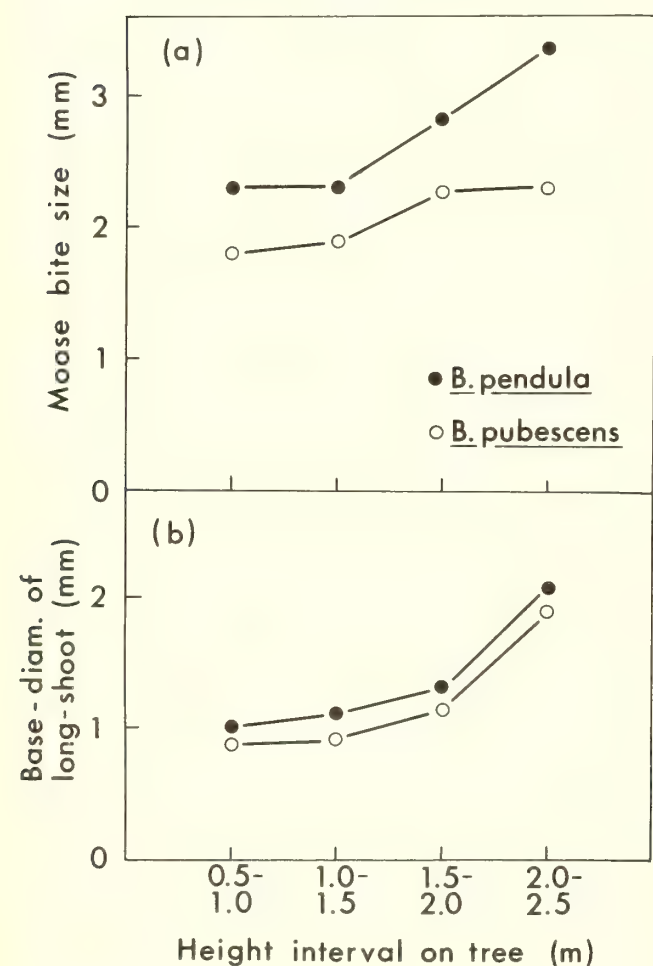


Figure 7.--Mean diameter of moose bites (a) and mean base diameter of long-shoots (b) on 2.5- to 3.0-m high birches exposed to moose browsing during one winter.

bite diameter increases more twig biomass is harvested, but at the same time the bite composition changes (Palo and others 1984). With increasing twig diameter the proportion of wood increases, while the proportion of buds decreases (fig. 8). However, the proportion of bark is more or less the same. Occurrence of phenols and other secondary metabolites in birch may deter the intake of fine twigs while fiber content may deter the intake of coarse twigs. Presumably, moose select food in a way that minimizes intake of harmful metabolites and fiber (Palo and others 1984). Phenols may constitute a major chemical defense against browsing vertebrates by reducing digestibility and increasing toxicity (Palo and others 1985). For a review of secondary metabolites in birch see Palo (1984).

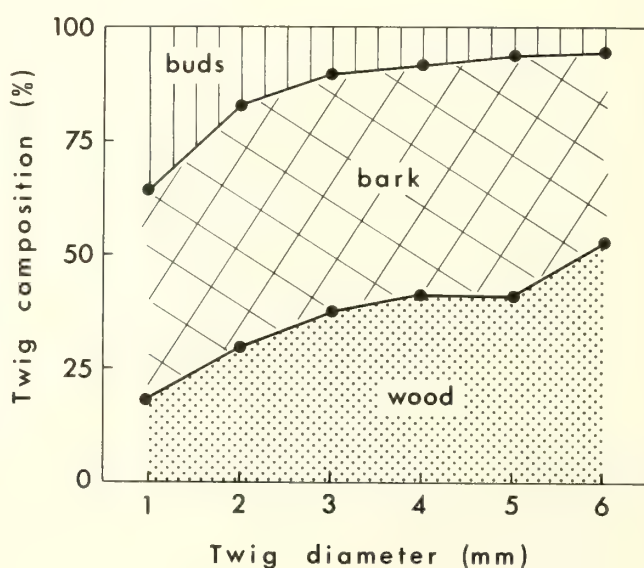


Figure 8.--The relative composition of 1- to 6-mm *Betula pendula* winter twigs (after Palo and others 1984).

Measurement of moose bite diameters revealed that larger bites were taken from higher levels on the tree than from lower levels (Danell 1983). When moose browsed *B. pendula*, the mean bite diameter was generally somewhat larger than on *B. pubescens* (Danell 1983; Rostad 1983). As the browsing itself can change shoot size, we conducted a field experiment in which unbrowsed birches, as similar as possible, of the two species were exposed to free-roaming moose at test stations during one winter (fig. 7). Here we again found that the bite diameter increased with increased height on the tree; there were also larger bite diameters on *B. pendula*. Interestingly, there is a close relation between these patterns and the mean shoot size (figs. 7a, b). It is not yet known whether this relation is due to chemical or mechanical properties.

RESPONSES OF BIRCHES TO MOOSE BROWSING

The vegetative and generative responses of birches to browsing have been studied on naturally browsed birches (Danell 1983; Danell and Huss-Danell 1985; Danell and others 1985). In more detailed studies of the responses due to winter browsing by moose, birches were clipped (Gröning 1980; Bergström and Danell 1985; Danell and Huss-Danell 1985; Danell and others 1985). The birch responses (tables 4 and 5) were, among other things, dependent on the intensity (proportion of biomass removed) and the frequency (number of winters browsed) of moose browsing. For simplicity, we here consider "moose browsing" as the removal of approximately 50 per cent of the long-shoots produced during the last summer.

Moose browsing leads to a prolonged growing season; bud abortion occurs later on trees affected by natural or simulated browsing. A somewhat higher mortality has been noted for terminal shoots on browsed birches than unbrowsed ones in northernmost Sweden after an extremely hard winter (K. Danell, unpublished observation). It is likely that these shoots on browsed birches were not fully prepared for the winter.

Height as well as stem diameter are negatively affected by moose browsing.

The number of long-shoots produced by a tree during the growing season following the winter when it was browsed was lower on browsed trees than on unbrowsed ones of the same age (fig. 9a). With increased browsing the proportion of branched long-shoots increased (fig. 9b). Short-shoots can be converted into long-shoots after browsing; this response was more frequent in open habitats than in shaded ones. However, this change in shoot type seldom compensates for high losses of long-shoots following moose browsing.

Shoot biomass will only occasionally be higher on birches affected by browsing than on unbrowsed ones (fig. 10). In most cases we measured either no change or decreased shoot production. Apart from the intensity and frequency of browsing, the production of long-shoots is also affected by competition from other birches. We found a

negative correlation between the shoot biomass produced by *B. pubescens* after heavy simulated browsing during three winters and the number of stems in the neighborhood (stand density) (fig. 11).

Since browsing reduces height growth, the long-shoots on browsed birches will be produced at lower levels than on intact ones. On unbrowsed birches the shoots will grow farther out of reach for moose each year. For example, on a 4-m high birch the majority of the shoots within the 1- to 2-m height interval are small sized and unfavorable for moose browsing. So, even if browsing does not change the biomass of shoots produced per tree, more shoots can be available for moose on birches previously browsed (Danell 1983). The fewer but larger shoots available on such trees also make harvesting easier.

Table 4.--Vegetative and generative responses of birches following natural or simulated moose browsing during winter. Data on *Betula pendula* and *B. pubescens* from different studies are summarized (Gröning 1980; Danell 1983; Bergström and Danell 1985; Danell and Huss-Danell 1985; Danell and others 1985). Increases are marked with (+) and decreases with (-). No change is indicated by (=)

Vegetative responses	
On the tree level:	
Length of growing season	(+)
Height and stem diameter growth	(-)
Number of long-shoots	(-)
Frequency of branched long-shoots	(+)
Conversion of short-shoots into long-shoots	(+)
Shoot biomass produced	(+) (=) (-)
Shoot biomass available for moose	(+)
Total number of winter buds on long-shoots	(-)
On the shoot level:	
Shoot size	(+)
Number of leaves	(+)
Number of winter buds	(+)
Shoot chemistry	(See table 5)
On the leaf level:	
Leaf size	(+)
Green leaf color	(+)
Leaf chemistry: chlorophyll concentration	(+)
nitrogen concentration	(+)
carbon:nitrogen ratio	(-)
Generative responses	
Number of catkins per tree	(-)
Individual seed weight	(+)

The responses in shoot biomass produced are strongly dependent on browsing intensity and frequency as well as habitat conditions.

Table 5.--Changes in birch winter shoot quality as a response to natural or simulated moose browsing. Data from *B. pendula* and *B. pubescens* collected in different studies (Bergström and Danell 1985; Danell and Huss-Danell 1985; Danell and others 1985). Increases are marked with (+) and decreases with (-). No change is indicated by (=)

Item ¹	Natural browsing		Simulated browsing					
	whole shoots		whole shoots		2 mm shoots			
	B. pe ²	B. pu	B. pe		B. pu		B. pe	B. pu
			I	III	I	III		
Na		=	=	=	=	-	=	=
K		=	=	=	=	=	-	=
Ca		-	-	=	=	-	=	=
Mg		-	=	-	=	=	-	=
P		=	=	-	=	=	=	-
N	=	=	=	-	=	=	=	=
Crude fat	-	-	-	=	-	-	=	=
Crude fiber		=	+	+	+	+	+	+
Phenols			=		=			
Water solubles			-		-			
Digestibility (IVOMD)			-	=	-	=	=	=

¹All items are compared in terms of per cent of dry mass.

²B. pe = *Betula pendula*; B. pu = *B. pubescens*; shoots collected after 1 year (I) or 3 years (III) treatment.

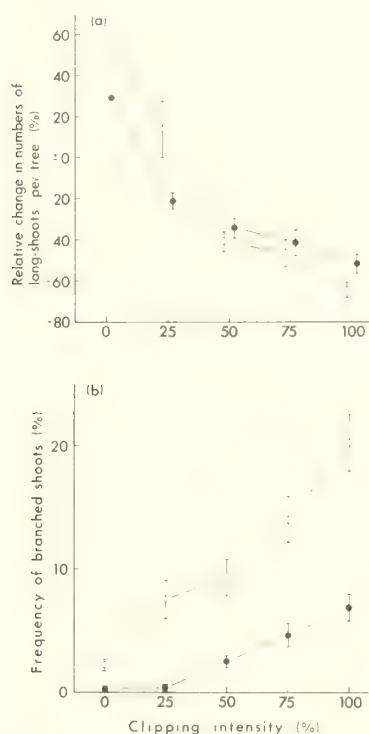


Figure 9.--Effects of different intensities of simulated browsing on the total number of current long-shoots per tree (a) and the frequency of branched long-shoots (b) on *Betula pendula* (●) and *B. pubescens* (○). The responses are from birches 1.6 and 2.6 m high, respectively, clipped during one winter only. Mean + S.E. given for N = 19-20. (The sampling procedure for estimation of control values (0) in figure 9a does not allow calculation of precision estimates.) For details see Bergström and Danell (1985).

With increasing browsing intensity during winter, the individual shoots produced the following summer increased in size (fig. 12). There were also more leaves per shoot and winter buds. Even if the number of buds per shoot increases as a response to browsing, it cannot compensate for the loss of buds through the decreased number of long-shoots at medium and high browsing intensities. At these browsing pressures the total reserve of buds on long-shoots is reduced from year to year.

The changes in shoot quality due to browsing are more complex. In addition to the effect of

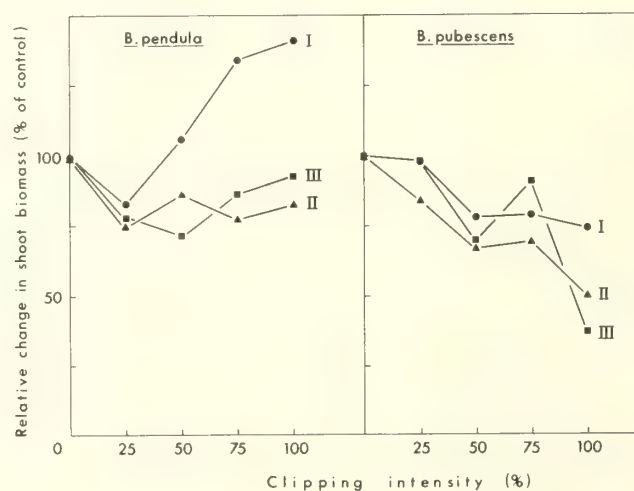


Figure 10.--Effects of different intensities of simulated browsing on the total dry mass of long-shoots produced per tree after treatments during one (I), two (II) and three (III) winters. For details see Bergström and Danell (1985).

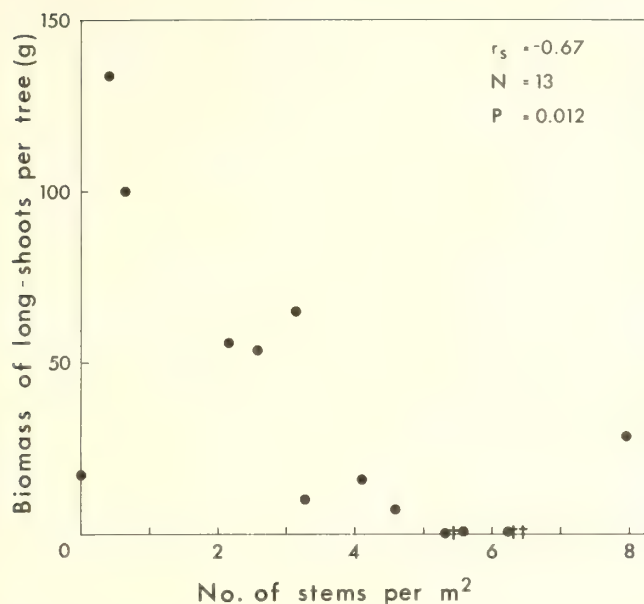


Figure 11.--Dry mass of long-shoots produced by *Betula pubescens* exposed to 100 per cent clipping (removal of all long-shoots produced during the previous summer) during three winters. The individual biomass for 13 birches still alive (●) is correlated with the number of other stems in the neighbourhood. When the three dead (+) individuals are included the corresponding statistics are $r_s = -0.71$, $N = 16$, $P = 0.002$. For details see Bergström and Danell (1985).

browsing intensity and frequency, shoots enlarge with increased browsing.

Therefore, discussion of quality changes must include whole shoots as well as fixed diameters (here we have chosen the 2-mm limit).

Data on whole shoots from birches affected by natural or simulated browsing (table 5) show decreased concentrations of Ca, Mg, crude fat, and water solubles in two or more of the samples or experiment groups. Likewise, increased fiber content and decreased digestibility occur. On the other hand, when we consider the 2-mm shoots, only lignin and the fiber content are similar to the whole shoot fraction. We therefore suggest that most of the changes found when we compare whole shoots from browsed and unbrowsed birches are due to the difference in shoot size between the groups. Data presented in figure 8 show an increase in the wood component and a decrease in the bud component when the shoot diameter increased from 1 to 4 mm.

Individual leaf area increased with increased browsing intensity and the leaves were greener. The leaves on previously browsed birches were richer in chlorophyll and nitrogen and had a lower C:N ratio than leaves from unbrowsed birches. Moderately browsed birches often carried a higher load of invertebrate herbivores (ants, psyllids, leaf-miners, and other leaf-eating insects) than intact birches. Leaves from such affected birches were more palatable to a generalized herbivore

(*Ariania arbustorum* (L.)) (K. Danell, unpublished observations).

With increased browsing intensity, the number of catkins per tree decreased but the individual seed weight increased in *B. pubescens*.

The responses of birches to moose browsing during winter are to a large extent growth responses (such as prolonged growing season and shoot enlargement). The pattern of responses indicates that the birches allocate more effort to growth than reproduction by reducing seed production. At the moment, it is difficult to argue that some of the responses are specific to moose browsing. What we have documented are most likely an array of general responses to mechanical damages of abiotic (such as stem breakage by snow) and biotic (such as herbivory) nature. Inter- and intraspecific competition are important features in many plant populations. Height growth is therefore extremely important for young trees; it helps to grow above the competitors and out of the reach of mammalian herbivores.

RESPONSES OF MOOSE TO BIRCHES PREVIOUSLY BROWSED

Studies of individually tagged *B. pendula* and *B. pubescens* demonstrated that browsed birches have a greater probability of being browsed the next winter than previously unbrowsed birches (Bergström 1983; Danell and others 1985). One possible explanation of this is that it reflects the availability of individual birches in the moose habitat. The browsed birches may be closer to pathways used by moose. We therefore set up a field experiment in northern Sweden (within a forest area of 140 km²) where we placed cut 2.5- to 3.0-m high birches, unbrowsed or slightly browsed and moderately browsed, of the two species side by side (Danell and others 1985). Fifty stations were set up in late October and revised in late May the following year. At stations where the consumption of twig biomass from the trees had been low, about 80 and 90 percent of *B. pendula* and *B. pubescens*, respectively, were taken by moose from the birches earlier browsed. At stations with medium or high biomass removal, approximately equal amounts were taken from the unbrowsed/slightly browsed and moderately browsed birches.

The higher palatability to moose of previously browsed birches may be due to strong individual differences in palatability between birches. It is possible that moose select some birches and then browse on them for several winters irrespective of changes due to the browsing itself. Therefore we conducted another field experiment where we selected pairs of unbrowsed *B. pubescens* that were as similar as possible (Danell and others 1985). We randomly chose one individual in each pair and simulated moose winter browsing on this birch, while the other was left as a control. During the following summer the treated birches responded by producing larger shoots etc. After the next winter we compared utilization by moose of the two types of birches. There were a higher frequency of moose bites, a larger moose bite diameter, and

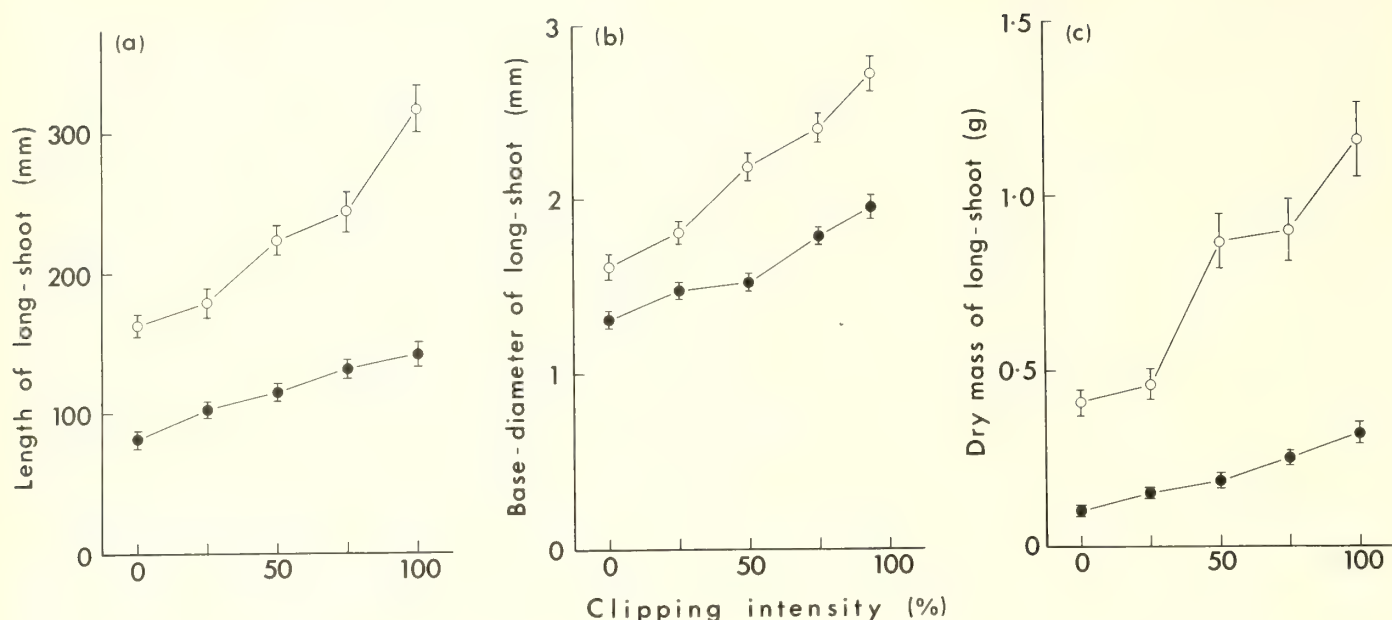


Figure 12.--Effects of different intensities of simulated browsing on the length (a), base diameter (b) and dry mass (c) of the individual current long shoots of *Betula pendula* (●) and *B. pubescens* (○). Mean $\pm$ S.E. given for N = 18-20. For details see legend to figure 9 and Bergström and Danell (1985).

about five times more twig biomass removed from the treated trees compared to the control trees.

CONCLUSIONS

For some reason, the birches previously browsed are more attractive to moose than unbrowsed ones. One explanation is that they are easier to harvest due to the relatively few but large shoots and their distribution. Other explanations are that shoots on trees responding to browsing are more palatable due to decreased concentrations of deterrent compounds, or due to increased concentrations of compounds acting as attractants. When moose browse on birches that have larger shoots, mean bite diameter generally increases and we can expect that the animals get less Ca, Mg, crude fat (resins), and water solubles, but more fiber per kilogram dry mass consumed (table 5). The overall effect on food quality is difficult to evaluate, but it is likely that digestibility decreases slightly. It is questionable if the advantage of affected birches being easier to harvest compensates for their decreased digestibility. On the other hand, if moose only slightly increase the bite diameter, the qualitative differences between browsing on previously browsed and unbrowsed birches are of a lower magnitude.

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REFERENCES

- Arnborg, T. Om vårtbjörkens och glasbjörkens ståndortskrav. Skogen (Stockholm) 33: 163-165; 1946. In Swedish.
- Bergström, R. Rebrowsing on birch (*Betula pendula* and *B. pubescens*) stems by moose. *Atces*. 19: 3-13; 1983.
- Bergström, R. 1986. Unpublished observations on file at the Research Unit of the Swedish Sportsmen's Association, Uppsala, Sweden.
- Bergström, R.; Danell, K. Effects of repeated simulated moose browsing on morphology, biomass and chemistry of two birch species. 1985. Unpublished report on file at the Research Unit of the Swedish Sportsmen's Association, Uppsala, Sweden.
- Bergström, R.; Hjeljord, O. Moose and vegetation interactions in northwestern Europe and Poland. Swedish Wildlife Research. In press.
- Cederlund, G.; Håkngren, G. The development of the Swedish moose population, 1970-1983. Swedish Wildlife Research. In press.

- Danell, K. Shoot growth of *Betula pendula* and *B. pubescens* in relation to moose browsing. *Alces*. 18: 197-209; 1983.
- Danell, K. 1986. Unpublished observations on file at the Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Umeå, Sweden.
- Danell, K.; Bergström, R.; Dirke, K. Moose browsing on juvenile and adult birches (*Betula pendula* and *B. pubescens*): test of a hypothesis on chemical defence. In: Proceedings of the 16th international congress of game biologists, September 25 - October 2, Strbske Pleso, Czechoslovakia. In press.
- Danell, K.; Ericson, L. Foraging by moose on two birch species when occurring in different proportions. *Holarctic Ecology*. 9: 79-84; 1986.
- Danell, K.; Huss-Danell, K. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos*. 44: 75-81; 1985.
- Danell, K.; Huss-Danell, K.; Bergström, R. Interactions between browsing moose and two species of birch in Sweden. *Ecology*. 66: 1867-1878; 1985.
- Fries, J. Yield of *Betula verrucosa* Ehrh. in middle Sweden and southern north Sweden. *Studia Forestalia Suecica*. 14: 1-303; 1964. In Swedish, with English summary.
- Hultén, E. Atlas of the distribution of vascular plants in northwestern Europe. Stockholm, Sweden: Generalstabens litografiska anstalts förlag; 1971. 531 p. In Swedish, with English summary.
- Gröning, P. Simulerat bete på vårtbjörk samt morfologi och fenologi hos några viltbetesarter. Uppsala, Sweden: Meddelanden från Växtbiologiska Institutionen; 1980: 4. In Swedish.
- Löyttyniemi, K.; Piisilä, N. Moose (*Alces alces*) damage in young pine plantations in the Forestry Board District Uusimaa-Häme. *Folia Forestalia*. 553: 1-23; 1983. In Finnish, with English summary.
- Löyttyniemi, K.; Rousi, M. On insect damage in young deciduous stands. *Folia Forestalia*. 384: 1-12; 1979. In Finnish, with English summary.
- Näslund, B.-Å. 1986. Unpublished observations at the Department of Silviculture, Swedish University of Agricultural Sciences, Umeå Sweden.
- Nyström, A. Selection and consumption of winter browse by moose calves. *Journal of Wildlife Management*. 44: 463-468; 1980.
- Nyström, A. 1986. Unpublished observations on file at the Grimsö Research Station, Riddarhyttan, Sweden.
- Palo, R. T. Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *Journal of Chemical Ecology*. 10: 499-520; 1984.
- Palo, R. T.; Sunnerheim, K.; Danell, K.; Bergström, R. Biomass and defensive chemicals in wood, bark and buds of birch (*Betula pendula* Roth.) of different twig diameters - Implications for browsers. In: Abstracts of the second international moose symposium; August, 21-25, Uppsala, Sweden: Swedish University of Agricultural Sciences; 1984. 52 p.
- Palo, R. T.; Sunnerheim, K.; Theander, O. Seasonal variation of phenols, crude protein and cell wall content of birch (*Betula pendula* Roth) in relation to ruminant in vitro digestibility. *Oecologia (Berlin)*. 65: 314-318; 1985.
- Raulo, J. Development of dominant trees in *Betula pendula* Roth and *Betula pubescens* Ehrh. *Communicationes Instituti Forestalis Fenniae*. 90: 4; 1977.
- Rostad, H. Beitepreferanse hos elg - forskjeller mellom dunbjørk (*Betula pubescens* Ehrh.) og hengebjørk (*B. verrucosa* Ehrh.) Ås, Norway: Hovedoppgave ved Institutt for skogskjøtsel, Norges landbrukshøgskole; 1983. In Norwegian.
- Stålfelt, F. Investigation of browsing on the shrub vegetation in an area of Värmland. *Zoologisk Revy (Stockholm)*. 32: 67-70; 1970. In Swedish, with English summary.
- Vivås, H. Winterbrowsing of the moose. *Swedish Wildlife Research*. In press.
- Westman, H. The damage caused by elk to young stands. *Bulletin* 28. Stockholm, Sweden: Royal School of Forestry; 1958: 1-148. In Swedish, with English summary.

INTRASPECIFIC VARIATION IN MOOSE PREFERENCE FOR WILLOWS

Kenneth L. Risenhoover

ABSTRACT: Moose (*Alces alces*) preferences for Alaskan feltleaf willow (*Salix alaxensis*) and grayleaf willow (*Salix glauca*) were compared among different habitats in Denali National Park and Preserve, AK, during the winter-spring period. Observations during the searching phase of diet selection indicate that moose are selective browsers, and feed on only a fraction of the plant stems available. Moose preferences for individual willow species varied considerably among habitat types, and did not appear to be related to the availability of biomass. Observed variations in willow preference could not be attributed to plant nutritional quality, or to the amounts of phenols and condensed tannins they contained. Further descriptive studies of *Salix* chemistry using more specific assays will be necessary to adequately test hypotheses explaining intraspecific variation in willow preference by herbivores.

INTRODUCTION

Willows (*Salix* spp.) are a primary food source for moose throughout much of their range, and are therefore considered an important component of moose habitat. In some areas, willows may comprise up to 95 percent of moose winter diets (Peek 1974; Penner 1978; Risenhoover unpublished data). However, despite the obvious importance of willows to moose and other herbivores, and the recognition that moose preferences for individual willow species may vary regionally (Milke 1969; Peek 1974; Penner 1978), there have been surprisingly few studies investigating the underlying reasons for variations in willow preference.

Preliminary results from studies of moose winter foraging strategies and resource use in Denali National Park and Preserve (DNPP), AK, (Risenhoover, in preparation) indicate that moose preferences for individual willow species are not consistent among habitat types. Possible explanations for the observed variations in willow preference include: (1) Individual plants within and between habitats vary in their chemical composition and therefore palatability to moose. (2) Species preferences are determined by the availability of alternative diet species, and their relative value to moose. (3) Species preference is a function of its abundance and the economics of feeding on it relative to other available forage.

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In this paper, I attempt to evaluate moose preferences for two widely distributed willows in DNPP, feltleaf willow and grayleaf willow, and examine possible reasons for the observed variations in moose preferences for individual plant species among habitats.

STUDY AREA AND METHODS

DNPP is located in central Alaska (60°40'N., 149°20'W.) bordering the Alaska Range, about 240 km south of Fairbanks (fig. 1). The study area consisted of the eastern portion of the park between the Teklanika and Nenana Rivers. Habitats in the study area are mountainous; U-shaped glacial valleys are drained by the Savage and Sanctuary Rivers, and by Riley Creek. Elevations range from 540 to 1,825 m; the majority of the study area occurs near treeline (about 760 m).

Vegetation types occurring in the study area are typical of the region and have been described by Viereck and Dyrness (1980) and by Van Cleve and others (1983). Open forest stands of primarily white spruce (*Picea glauca*) occur in the eastern portions of the study area, and in scattered patches or in strips along major creeks and rivers. Occasional stems of grayleaf willow, feltleaf willow, diamondleaf willow (*S. planifolia*) and



Figure 1.--Location of Denali National Park and Preserve in interior Alaska.

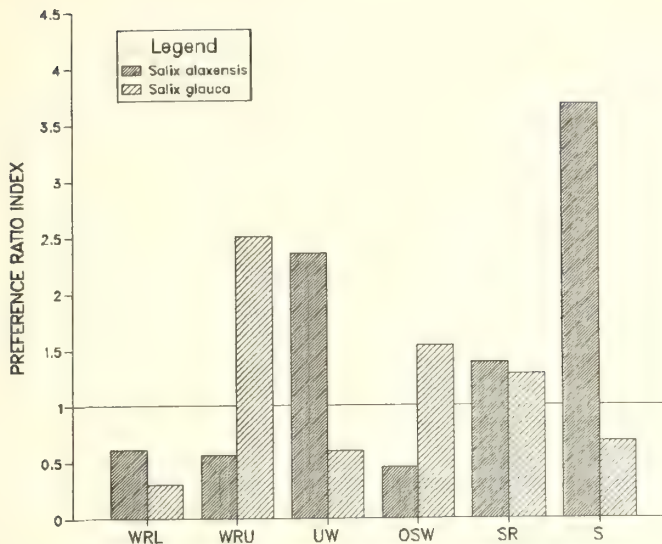


Figure 2.--Comparison of moose preferences for *Salix alaxensis* and *Salix glauca* in habitats in Denali National Park and Preserve, AK. (WRL=willow riparian lowland; WRU=willow riparian upland; UW=upland willow; OSW=open spruce willow; SR=spruce riparian; S=spruce).

resin birch (*Betula glandulosa*) may be present in the forest understory. Below treeline, willows and green alder (*Alnus crispa*) are most abundant along riparian zones. Above treeline, willows form dense thickets along riparian areas. For this study, vegetation in DNPP was subdivided into six habitat types based primarily on species composition and productivity (Risenhoover, unpublished data).

Moose diet selection and species preferences were determined in the different habitats in DNPP during January-April, 1983 and 1984. Sixteen moose were radio-collared and available for study. During foraging bouts (the periods of activity between bedding periods), free-ranging moose were followed at close range (<20 m) by two observers and all plant stems visited and the number of bites taken at each stem were recorded. In addition, moose search paths during foraging bouts were flagged, and the habitat volume within 1.5 m (the lateral reach of a moose) of the search path was sampled systematically using 3- by 3-m rectangular plots to determine the production biomass (grams/meter²) of potential food items available. Forage production and consumption by moose were calculated using twig diameter-length-weight regression equations developed for each species (Risenhoover, unpublished data). An average weight for both browsed and current annual growth twigs was calculated by measuring a minimum of 50 browsed and unbrowsed twigs on stems of all species available within the search volume.

Preference is demonstrated when certain resources are utilized more often than would be predicted from the frequency with which they are encountered in the environment. For this study, preference was estimated using the preference ratio index (P_i) given by the equation:

$$P_i = \frac{N_i / \sum N_j}{E_i / \sum E_j}$$

where N_i =the number of resource items i used; N_j =the total number of resource items used; E_i =the number of resource items i in the environment; and E_j =the total number of resource items in the environment. To control the large influence of rare species on this index, P_i values were not calculated for species that constituted less than 5 percent of the available biomass unless they made up more than 10 percent of the biomass consumed during the foraging bout.

Composite samples of current annual growth twigs from a minimum of 20 plant stems were collected from representative sites in each habitat type and analyzed to determine their apparent nutritional quality. Samples were dried at 60° C in a forced-draft drying oven and then ground twice in a Wiley mill (2-mm screen). Ground samples were stored in vapor-proof bags at -20° C until analyzed. The nutritional quality of forage samples was determined at the Animal Nutrition Laboratory, Michigan State University (East Lansing) according to AOAC procedures (Horwitz 1980). Gross energy (Kcals/g) was determined using an adiabatic bomb calorimeter. Crude protein ($N \times 6.25$) was determined by semi-microkjeldahl techniques. Percent ash was determined by burning in a muffle furnace at 650° C. In addition, the relative fiber components (cell walls, cell solubles, cellulose, hemicellulose, and lignin) of forage samples were determined according to procedures described by Goering and Van Soest (1970).

The apparent digestibility of forage samples was estimated using *in vitro* techniques described by Pearson (1970). Rumen innoculum was obtained from a yearling moose collected at the Moose Research Center (Kenai National Wildlife Refuge, AK) that had been feeding on native forages. Forage samples were tested in triplicate. The apparent digestible energy of samples was calculated by multiplying the *in vitro* digestibility of forage samples by the gross energy $\times 0.85$ according to Hobbs and others (1981).

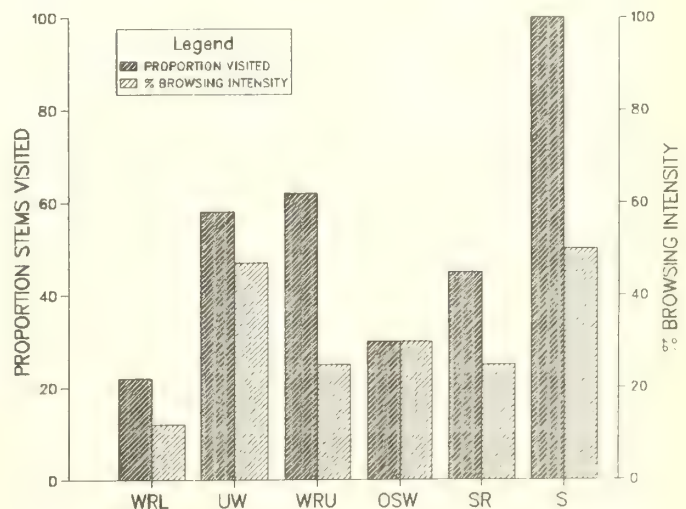


Figure 3.--Comparison of moose visitation patterns and utilization of *Salix alaxensis* stems in various habitat types in Denali National Park and Preserve, AK. (Abbreviations follow fig. 2).

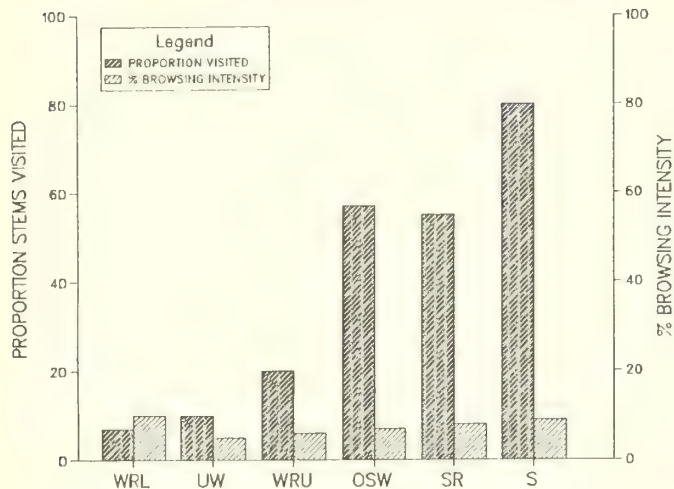


Figure 4.--Comparison of moose visitation patterns and utilization of *Salix glauca* stems in various habitat types in Denali National Park and Preserve, AK. (Abbreviations follow fig. 2).

Additional forage samples were collected, freeze-dried and analyzed to determine the total phenolic and condensed tannin fractions, and the ether-soluble component. Procedures for aqueous methanol extraction, and analyses for Folin-Dennis reactives and proanthocyanidins followed Martin and Martin (1982). Vanillin reactives were analyzed as described by Burns (1971) as modified by Price and others (1978), and astringent substances were analyzed by the hemoglobin precipitation method of Schultz and others (1981) using freshly collected sheep's blood as a source of hemoglobin. Concentrations of Folin-Dennis reactives and astringent substances were expressed as tannic acid equivalents; concentrations of vanillin reactives were expressed as catechin equivalents, and concentrations of proanthocyanidins were expressed as quebracho tannin equivalents.

RESULTS

Salix alaxensis was the major browse species in the winter diet of moose in DNPP and accounted for 44 percent of all biomass consumed during observed foraging bouts (Risenhoover, in preparation). *Salix glauca* was also an important species in moose winter diets and comprised 11 percent of the total biomass consumed. However, moose preferences for willows were not consistent among habitat types (fig. 2). Despite its importance in the diet, moose demonstrated a strong preference for *S. alaxensis* in only three of the six habitat types available. *Salix glauca* was also preferred in three of the six available habitat types.

Observations during the searching phase of diet selection indicate that moose were very selective browsers and fed on only a fraction of the *S. alaxensis* and *S. glauca* stems they encountered along their search path (figs. 3 and 4). Moose generally visited a higher proportion of available stems in habitats where species were preferred. In addition, there was a significant ($r=0.85$, $P<0.05$)

positive correlation between moose preference for *S. alaxensis* and the degree of browsing intensity (proportion of available twigs browsed by moose) observed on stems within habitats. In contrast, the average browsing intensity observed on *S. glauca* stems was similar among habitat types.

Preference and Production Biomass

Relationships between moose preferences for *S. alaxensis* and *S. glauca* and plant production biomass were compared to determine if the observed variations in moose preferences were density related (a functional response). Current ecological theory suggests that the degree of preference exhibited by a predator (in this case an herbivore) for a specific prey type may be dependent on the relative abundance of that prey and/or the other acceptable prey available (Emlen 1985). However, when moose preferences for *S. alaxensis* and *S. glauca* were compared to the total production biomass (grams/meter²) available, and to the abundance of *S. alaxensis* or *S. glauca* biomass, respectively, no significant relationships were detected (figs. 5-8).

Preference and Plant Chemistry

Analyses of forage samples collected from the various habitats indicated that the chemical composition of individual plants may vary greatly between areas (Risenhoover, in preparation). Correlations between moose preference values and the digestible energy, crude protein, and minerals in plant tissues were generally weak and not significant (table 1). Although there was a strong negative correlation between moose preference values and lignin content ($r = -0.624$), no significant ($P > 0.05$) correlations were detected between moose preferences and plant fiber content.

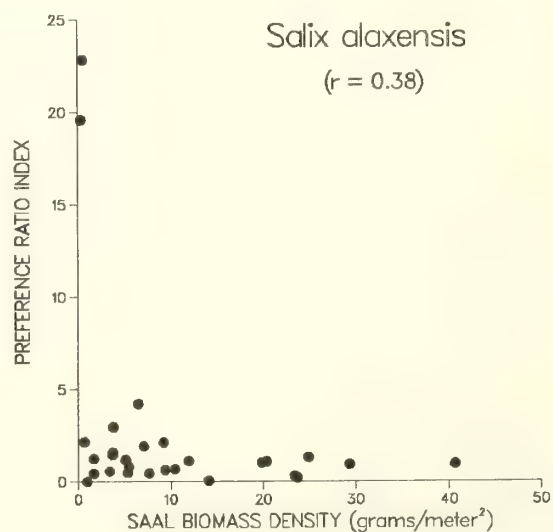


Figure 5.--Relationships between moose preference for *Salix alaxensis* and the density of *Salix alaxensis* production biomass.

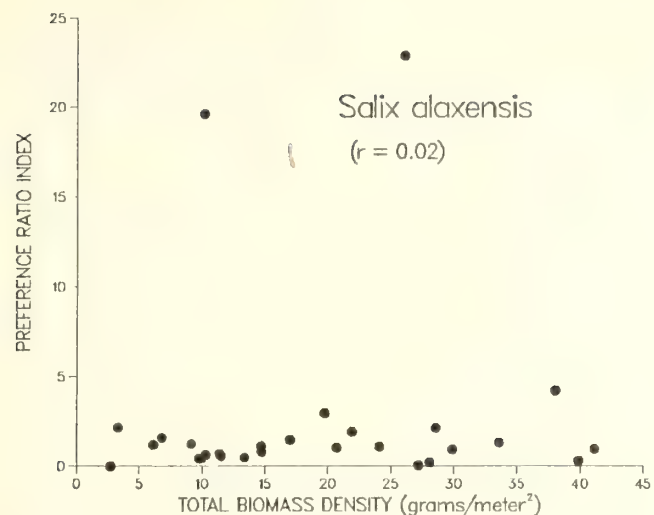


Figure 6.--Relationships between moose preference *Salix alaxensis* and total biomass density.

Overall, there was a negative relationship between moose preference and plant phenolic content. However, only the correlation between preference and astringent substances was significant ($r = -0.733$, $P < 0.05$). The correlation coefficient for proanthocyanidins was also strongly negative ($r = -0.601$), but was not significant. However, despite the significant negative relationship, variation in the astringency of willow samples from different habitats was small, and could explain only 54 percent of the variation in moose willow preference. Thus, it would seem unlikely that astringency alone is responsible for the observed variability in moose willow preference.

Within habitat types, it was not uncommon to find unbrowsed willow stems growing alongside plants that had been heavily utilized by moose (Risenhoover,

in preparation). We compared pooled twig samples from 20 browsed and unbrowsed stems in an attempt to evaluate any possible chemical differences between plants used and avoided by moose. No significant differences were detected in the chemical characteristics of browsed and unbrowsed plant tissues (table 2).

DISCUSSION

The forage selection patterns of moose in DNPP strongly suggest that there are important differences in the relative value of willows growing within different habitats. Direct observations of moose selectivity and browse utilization patterns within habitats also support this hypothesis. However, our preliminary analysis clearly favors rejection of all three possible explanations for the observed intraspecific variation in moose preferences for willows.

It is possible that the variations in willow preference observed between habitats were due to errors in our assessment of diet and forage availability. Indeed, diet preference and selectivity are particularly difficult to assess under field conditions. However, in this study, differences in willow preference between habitat types were pronounced and mostly consistent. The methods employed in this study allowed observers to quantify diet selection with a high degree of precision. Further, since our assessment of forage availability was limited to the actual search volume traversed by the moose, we are confident that our estimates of relative forage availability provide an accurate portrayal of what was actually available to the foraging moose.

Therefore, despite the lack of strong supportive evidence, the most likely explanation for the observed differences in preference remains that moose were selecting stems on the basis of plant

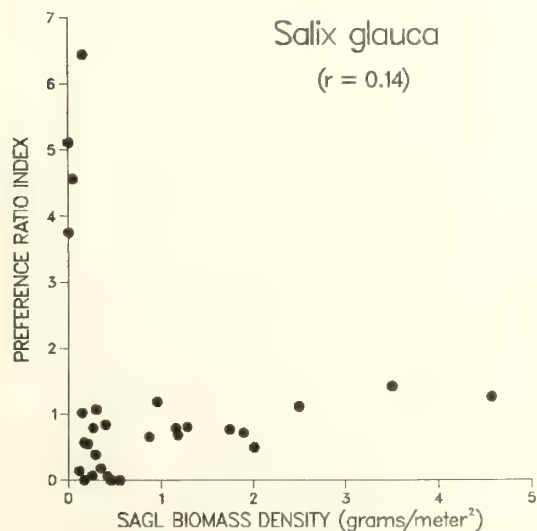


Figure 7.--Relationships between moose preference for *Salix glauca* and the density of *Salix glauca* production biomass.

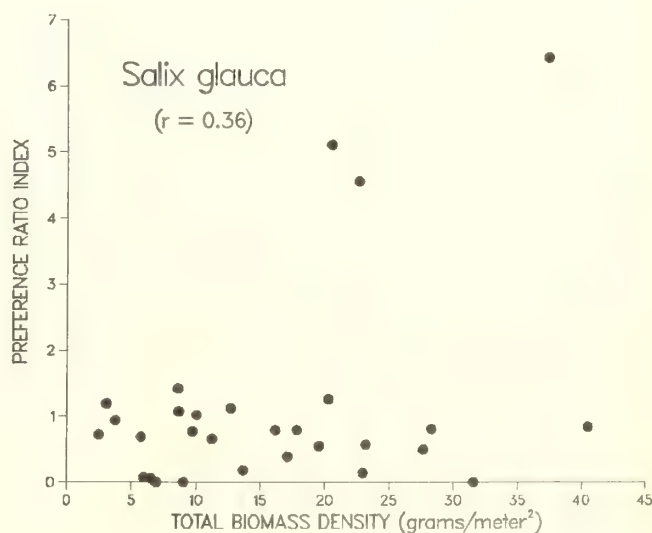


Figure 8.--Relationships between moose preference for *Salix glauca* and total biomass density.

Table 1.--Correlation coefficients (r) between moose preference ratio values and the concentrations of nutrients, fiber and phenols present in Salix alaxensis and Salix glauca plant tissues in Denali National Park and Preserve, AK

Chemical characteristic	Correlation coefficient ¹
Digestible energy	-0.351
Crude protein	-0.387
Ash	-0.500
Ether extract	-0.027
Fiber components:	
Neutral detergent fiber	0.441
Acid detergent fiber	0.000
Lignin	-0.624
Cellulose	0.570
Hemicellulose	0.376
Phenolics:	
Astringent substances	-0.733**
Proanthocyanidins	-0.601
Vanillin reactive	0.168
Folin-Dennis reactive	-0.510

**Significant at P < 0.05.

¹Correlation coefficients were calculated from combined results for S. alaxensis and S. glauca.

characteristics that vary within, and possibly among willow species. Despite much recent interest (Palo 1984; Rowell-Rahier 1984; Bryant and others 1985; Palo and others 1985; Tahvanainen and others 1985; Waring and others 1985), our understanding of the antiherbivore chemistry of willows is still in its infancy, and it is possible that an important component in the chemical defense of these species has been overlooked in our analyses.

To date, phenolics are the only chemical class of secondary substances reported to occur within the family Salicaceae (Audette and others 1966; Palo 1984). Bryant (unpublished report) found a negative correlation between levels of plant phenols in S. alaxensis leaves during summer and their palatability and digestibility by snowshoe hare (Lepus americanus). However, in agreement with this study, Bryant found no relationship between winter plant phenols in woody twigs and hare palatability.

Although phenolic glycosides are commonly found in willows (Palo 1984; Rowell-Rahier 1984; Tahvanainen and others 1985), and are known to be antibacterial, Bryant (unpublished report) found no differences in concentrations of phenolic glycosides in palatable and unpalatable forms of S. alaxensis.

To date, there has been very little descriptive work completed on the ether-soluble fraction of Alaskan willows. Although the ether-soluble fraction of Alaskan willows is largely composed of lipids (Bryant and others 1985), it is possible that an, as yet, unidentified deterrent compound present in this fraction could be responsible for the observed variations in moose willow preference. For example, Reichardt and others (1984) showed that although snowshoe hare preferences for Alaskan paper birch (Betula resinifera) could not be explained by gross chemical fractions (ether extracts or phenols), they clearly demonstrated that hare preferences were related to the distribution of specific resinous phytochemicals present in birch stems. Further descriptive studies of Salix chemistry using more specific assays will be necessary to adequately test the plant chemistry hypothesis.

The intraspecific variations in moose preference for willows observed during this study indicate that moose-forage relations in DNPP are complex and poorly understood. While considering each plant species as a biological unit may simplify the description of moose-plant relationships, it may obscure important aspects of moose food-seeking behavior and diet preference (Risenhoover, in preparation). Accurate descriptions of herbivore diet preferences and herbivore-plant relations will require the consideration of intraspecific variation in herbivory across geographic ranges.

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Table 2.--Comparison of the chemical composition of browsed and unbrowsed Salix alaxensis from the willow riparian lowland habitat type

	Digestible energy	Crude protein	Acid detergent fiber	Neutral detergent fiber	Percent lignin	Percent ash
Browsed	2.14	8.22	41.3	53.3	17.1	2.11
Unbrowsed	2.33	8.20	40.7	54.5	17.3	2.34

REFERENCES

- Audette, R. C. S.; Blunden, G.; Steel, J. M.; Wong, C. S. Thin layer chromatography of phenolic glycosides and its use for screening procedure for the genus Salix. J. Chromatogr. 25: 367-372; 1966.
- Bryant, J. P.; Wieland, G. D.; Clausen, T.; Kuropat, P. Interactions of snowshoe hare and feltleaf willow in Alaska. Ecology. 66: 1564-1573; 1985.
- Bryant, J. P. Unpublished report on file at: Institute of Arctic Biology, University of Alaska, Fairbanks, AK.
- Burns, R. E. Method for estimation of tannin in grain sorghum. Agron. J. 63: 511-512; 1971.
- Emlen, J. M. Population biology: the coevolution of population dynamics and behavior. New York: MacMillan; 1985. 547 p.
- Goering, H. K.; Van Soest, P. J. Forage fiber analysis. Agric. Handbk. 379. Washington, DC: U. S. Department of Agriculture, Agricultural Research Service; 1970. 20 p.
- Hobbs, N. T.; Baker, D. L.; Ellis, J. E.; Swift, D. M. Composition and quality of elk winter diets in Colorado. J. Wildl. Manage. 45: 156-171; 1981.
- Horwitz, W. ed. Official methods of analysis of the Association of Official Analytical Chemists. Washington, DC: Association of Official Analytical Chemists; 1980. 1018 p.
- Martin, J. S.; Martin, M. M. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. Oecologia. 54: 205-211; 1982.
- Milke, G. C. Some moose-willow relationships in the interior of Alaska. Fairbanks, AK: University of Alaska; 1969. 76 p. Thesis.
- Palo, R. T. Distribution of birch (Betula spp.), willow (Salix spp.) and poplar (Populus spp.) secondary metabolites and their potential role as chemical defense against herbivores. J. Chem. Ecol. 10: 499-520; 1984.
- Palo, R. T.; Sunnerheim, K.; Theander, O. Seasonal variation of phenols, crude protein and cell wall content of birch (Betula pendula Roth.) in relation to ruminant in vitro digestibility. Oecologia 65: 314-318; 1985.
- Pearson, H. A. Digestibility trials: in vitro techniques. In: Proceedings, range and wildlife habitat evaluation: a research symposium. Misc. Publ. 1147. Washington, DC: U. S. Department of Agriculture, Forest Service; 1970: 85-92.
- Peek, J. M. A review of moose food habits studies in North America. Nat. Can. 101: 195-215; 1974.
- Penner, D. M. Some relationships between moose and willow in the Fort Providence, N.W.T. area. Edmonton: University of Alberta; 1978. 183 p. Thesis.
- Price, M. L.; Van Scoyoc, S.; Butler, L. G. A critical review of the vanillan reaction as an assay for tannin in sorghum grain. J. Agric. Food Chem. 26: 1214-1218; 1978.
- Reichardt, P. B.; Bryant, J. P.; Clausen, T. P.; Wieland, G. D. Defense of winter-dormant Alaska paper birch against snowshoe hares. Oecologia. 65: 59-69; 1984.
- Risenhoover, K. L. Winter foraging and survival strategies of moose inhabiting subarctic and boreal forest habitats. Houghton, MI: Michigan Technological University; in preparation. Dissertation.
- Risenhoover, K. L. Unpublished data, Houghton, MI: Department of Biological Sciences, Michigan Technological University; 1984.
- Rowell-Rahier, M. The presence or absence of phenolglycosides in Salix (Salicaceae) leaves and the level of dietary specialization of some of their herbivorous insects. Oecologia. 62: 26-30; 1984.
- Schultz, J. C.; Baldwin, I. T.; Nothnagle, P. J. Hemoglobin as a binding substrate in quantitative analysis of plant tannins. J. Agric. Food Chem. 29: 823-826; 1981.
- Tahvanainen, J.; Helle, E.; Julkunen-Tiitto, R.; Lavola, A. Phenolic compounds of willow bark as deterrents against feeding by mountain hare. Oecologia. 65: 319-323; 1985.
- Van Cleve, K.; Dyrness, C. T.; Viereck, L. A.; Fox, J.; Chapin, F. S. III; Oechel, W. Taiga ecosystems in interior Alaska. BioScience. 33: 39-44; 1983.
- Viereck, L. A.; Dyrness, C. T. A preliminary classification system for vegetation of Alaska. Gen. Tech. Rep. PNW-106. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1980. 38 p.
- Waring, R. H.; McDonald, A. J. S.; Larsson, S.; Ericsson, T.; Wiren, A.; Arwidsson, E.; Ericsson, A.; Lohammer, T. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. Oecologia. 66: 157-160; 1985.

SAGEBRUSH (ARTEMISIA TRIDENTATA) MONOTERPENOID CONCENTRATIONS

AS FACTORS IN DIET SELECTION BY FREE-GRAZING SHEEP

Wilson K. Yabann, Elizabeth A. Burritt and John C. Malechek

ABSTRACT: Summer and fall grazing trials were conducted to study the effect of monoterpenoid concentrations on the diet selection of sheep grazing big sagebrush (Artemisia tridentata ssp. tridentata) range. Total monoterpenoid concentrations were significantly lower in browsed sagebrush plants than in rejected plants. Sheep selected older plants and plant parts, not current season's growth. As annual grasses in the community declined, sheep consumed more sagebrush, resulting in an increase in dietary crude protein but a decline in in vitro organic matter digestibility. This study indicates that monoterpenoid levels, not nutritional constituents, may influence sheep diet selection of sagebrush.

INTRODUCTION

Diet selection is a feature that has enabled grazing animals to survive on ranges with varying levels of food resources. Optimal foraging theory predicts that an animal will maximize its net energy intake while foraging. However, research has failed to demonstrate a consistent relationship between animal dietary preferences and the proximate composition of plants. Arnold and Dudzinski (1978) stated that animals are not capable of recognizing such entities as crude protein, crude fiber, energy, silica, or ash because these fractions do not exist in those forms at the molecular level in plant tissue. Researchers have correlated animal preferences with certain secondary compounds found in plant tissue (Bryant and Kuropat 1980; Provenza and Malechek 1984; Cooper and Owen-Smith 1985). In addition, bioassay techniques have been used to isolate compounds deterrent to herbivores (Bryant 1981; Bryant and others 1983; Reichardt and others 1984).

The poor palatability of both sagebrush and juniper (Juniperus spp.) species has been attributed to their monoterpenoid content (Dietz and Nagy 1976; Schwartz and others 1980).

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However, other researchers (Scholl and others 1977; Welch and others 1983; Behan and Welch 1985) have reported that such a relationship does not exist. The objectives of this study were to determine if monoterpenoid concentrations and nutritional constituents relate to dietary selection of big sagebrush (Artemisia tridentata ssp. tridentata) by sheep, and to examine the effects of seasonal variations in monoterpenoid concentrations and nutritive value of big sagebrush on dietary selection by sheep.

MATERIALS AND METHODS

The study was conducted at the Utah State University Tintic Valley Research Facility, located in Juab County, west-central Utah. Vegetation on the study site is dominated by big sagebrush (Artemisia tridentata ssp. tridentata) with a sparse understory consisting mainly of cheatgrass (Bromus tectorum) with lesser amounts of western wheatgrass (Agropyron smithii) and crested wheatgrass (Agropyron desertorum). Two 14-day grazing trials were conducted, one in mid-August and the other in mid-November. During each trial, a 0.06-ha paddock containing approximately 650 shrubs was grazed by 30 mature ewes. A new paddock was used for each trial. The resulting stocking rate of 1,344 animal unit days/ha was extremely heavy and was designed to achieve complete use of the understory and heavy utilization of sagebrush. Five of the ewes used in the trials were esophageally fistulated for the collection of dietary samples. All sheep used in the study had prior experience grazing big sagebrush.

Biomass of sagebrush was inferred from previous studies done in the same area (Narjisse 1981). Density of sagebrush plants was determined by counting all individuals in each pasture. Percent utilization of sagebrush was defined as either light (< 50 percent) or heavy ($\geq$ 50 percent) and was determined by ocular estimates.

Five days prior to each trial, sheep were placed in a holding paddock adjacent to the study area to familiarize them with the conditions of the experiment. During each trial, sheep were observed at distances of 2 m or less, and the following information was recorded: which individual sagebrush plants sheep browsed, the type of plant parts sheep consumed, how sheep consumed these parts, and which sagebrush whole plants and plant parts were avoided. From these

observations, selected plants were labeled either browsed or rejected. A browsed plant was defined as a plant that sheep were observed to sniff and select one or more bites from. Samples of browsed plants were taken in such a way as to simulate sheep browsing. Each browsed plant was paired with its closest totally rejected neighbor. A rejected plant was one that sheep were observed to sniff but did not browse. Hand-harvested parts from the rejected plants were as similar as possible to those parts collected from browsed individuals.

An analysis of the specific plant parts consumed or rejected from a browsed plant was also conducted. A browsed plant part was one representative of the portions of sagebrush sheep were observed to consume. Rejected plant parts were those portions of sagebrush that appeared to be consumable and sheep sniffed but did not consume. Also, any parts sheep removed from the plant but did not ingest (such as those dropped to the ground) were also classified as rejected.

Samples were collected at the same time of day to avoid possible diurnal variation in plant monoterpenoid concentrations. Upon collection, samples were sealed in plastic bags, placed on ice, and later frozen. Sample preparation and analysis for monoterpenoid concentrations followed the gas chromatography procedure of Welch and McArthur (1981). Subsamples of the hand-harvested material were freeze-dried, ground to pass a 40-mesh screen, and analyzed for Kjeldahl-N and in vitro organic matter digestibility (IVOMD) (Tilley and Terry 1963). In addition to hand-harvested samples, diet samples were collected on days 1,3,5 and 7 of each trial using esophageally fistulated sheep. These samples were freeze-dried, ground, and evaluated for Kjeldahl-N and IVOMD as described above.

Analysis of variance (Neter and Wasserman 1974) was used to compare treatments (browsed versus rejected plants and plant parts), seasons, and their interactions.

RESULTS AND DISCUSSION

Monoterpenoid concentrations were about 2.6 times higher in rejected plants than in browsed plants during summer (fig. 1). In fall, rejected plants contained 3.3 times the monoterpenoid concentrations of browsed plants. Monoterpenoid concentrations in plant parts followed similar trends, with rejected plant parts containing 5.9 and 3.3 times the monoterpenoid concentrations of browsed plant parts for summer and fall, respectively (fig. 2). In addition to higher monoterpenoid levels in rejected versus browsed forage, rejected forage generally contained twice as many individual monoterpenoid compounds as browsed forage. In general, sheep refused to consume plant parts that contained more than 0.33 percent monoterpenoids.

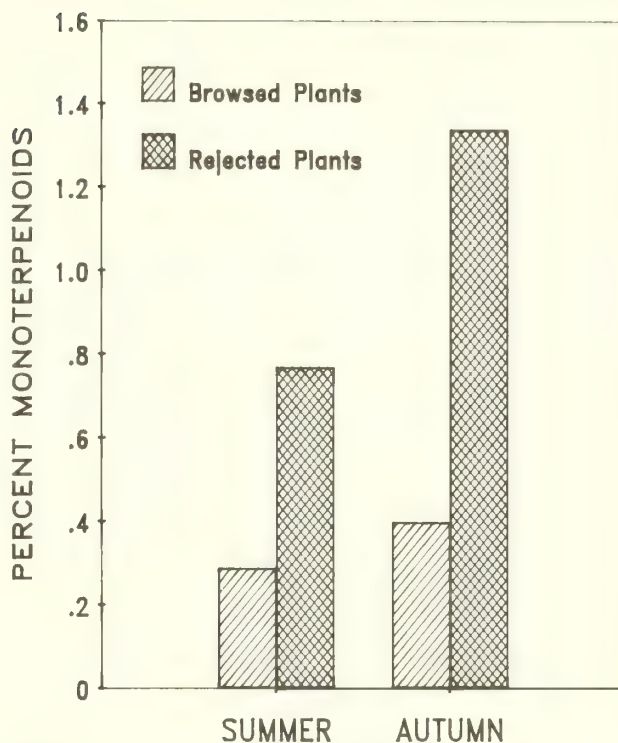


Figure 1.--Percent total monoterpenoid concentrations of browsed and rejected whole plants for summer and autumn, 1983 (LSD_{.05} = 0.31).

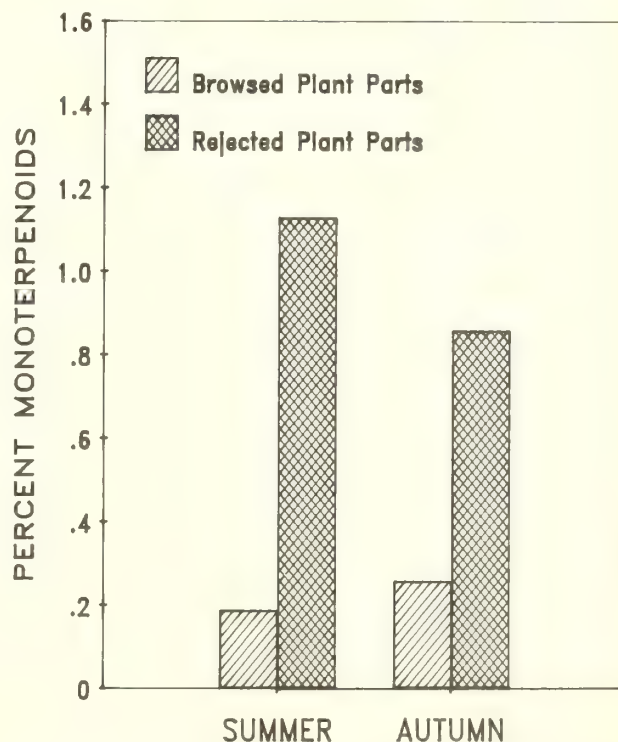


Figure 2.--Percent total monoterpenoid concentrations of browsed and rejected plant parts for summer and autumn, 1983 (LSD_{.05} = 0.17).

Correlative studies relating monoterpenoid concentrations to dietary habits are conflicting. Several researchers (Scholl and others 1977; Welch and others 1983; Behan and Welch 1985) reported that plant preferences exhibited by mule deer (*Odocoileus hemionus*) for different accessions of sagebrush were not related to total or individual monoterpenoid concentrations. Schwartz and others (1980) reported that in feeding trials comparing several species of juniper browse, deer preferred species lowest in oxygenated monoterpenoids. Results of studies using deer or other herbivores may not be directly applicable to sheep, because sheep and deer apparently prefer different taxa of sagebrush (Sheehy and Windward 1981). Narjisse (1981) reported that sheep discriminated against monoterpenoid odor while goats discriminated against monoterpenoid taste, implying genetic-based differences in sensory modalities and perceptions.

No seasonal differences in monoterpenoid concentrations were noted for browsed whole plants, but monoterpenoid concentrations were higher in rejected whole plants in fall than in summer. This is inconsistent with results reported by Narjisse (1981) and Cedarleaf and others (1983). They found higher sagebrush monoterpenoid concentrations in August than in November. However, their studies surveyed current season's growth and our study primarily involved older growth. The reported increase in whole plant monoterpenoid levels during fall in our study may have been due to heavier use of sagebrush in fall than summer, leaving fewer rejected sagebrush plants and therefore artificially elevating monoterpenoid levels. We found no differences in total monoterpenoid concentrations for summer- and fall-browsed plant parts, but concentrations were higher in summer than fall for rejected plant parts.

Despite uniform soil type and a homogeneous plant community on our study site, a high degree of variability existed in monoterpenoid concentrations among and within individual sagebrush plants (table 1). Narjisse (1981)

also observed a high degree of plant to plant variability in monoterpenoid concentrations of sagebrush. This variability probably accounted for complete consumption of some shrubs while others were completely rejected. Similarly, Wright (1970) reported that the palatability of three-tip sagebrush (*A. tripartita*) was so variable that some plants died due to overuse while others remained untouched.

Whether sheep were selecting against monoterpenoid concentrations or on the basis of some other constituent in sagebrush, they were selecting their diet at the expense of crude protein and digestibility. Crude protein content of big sagebrush on a whole plant basis was significantly higher in rejected (8.5 percent summer and 10.8 percent fall) than in browsed (7.2 percent summer and 8.2 percent fall) individuals (fig. 3). Similar trends were observed for rejected versus browsed plant parts (fig. 4). In fall, both rejected and browsed whole plants were statistically higher in crude protein than summer.

Digestibility followed trends similar to crude protein, although no differences existed between IVOMD of browsed and rejected whole plants in the summer (fig. 5). IVOMD was higher for rejected (58 percent) versus browsed (41 percent) whole plants in the fall trial. Rejected plant parts were significantly higher in IVOMD than browsed plant parts in summer and fall (fig. 6).

In general, sheep browsed older plants that were larger and had exfoliating bark, rejecting smaller, greener plants (fig. 7). In addition, sheep were observed to break twigs, ingest the older portion of the twig, and drop the younger growth. Sheep preferred older growth (previous years' twigs or exfoliating bark) to current season's growth, resulting in lower levels of dietary crude protein and digestibility (figs. 3-6) than they could have obtained had they consumed current season's growth. Provenza and Malechek (1984) reported that goats browsing blackbrush (*Coleogyne ramosissima*) preferred older growth to current season's growth despite

Table 1.--Percent range of monoterpenoids in individual sagebrush whole plants and plant parts¹

Season	Whole plants		Plant parts	
	Browsed	Rejected	Browsed	Rejected
-----Percent-----				
Summer	0.06 - 0.63	0.30 - 1.80	0.16 - 0.27	0.86 - 1.27
Fall	0.21 - 0.70	0.75 - 2.15	0.21 - 0.32	0.59 - 1.27

¹ percent monoterpenoids on a dry matter basis.

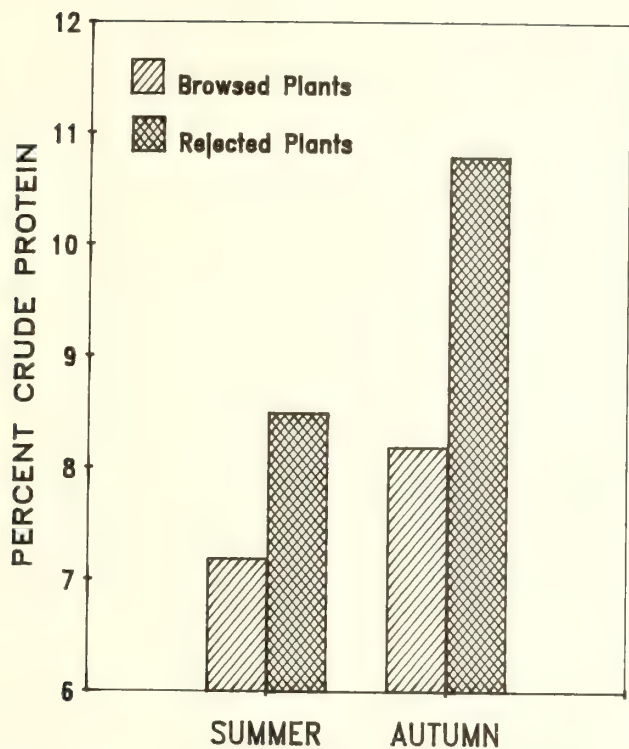


Figure 3.--Percent crude protein of browsed and rejected whole plants during summer and autumn, 1983 (LSD_{.05} = 0.62).

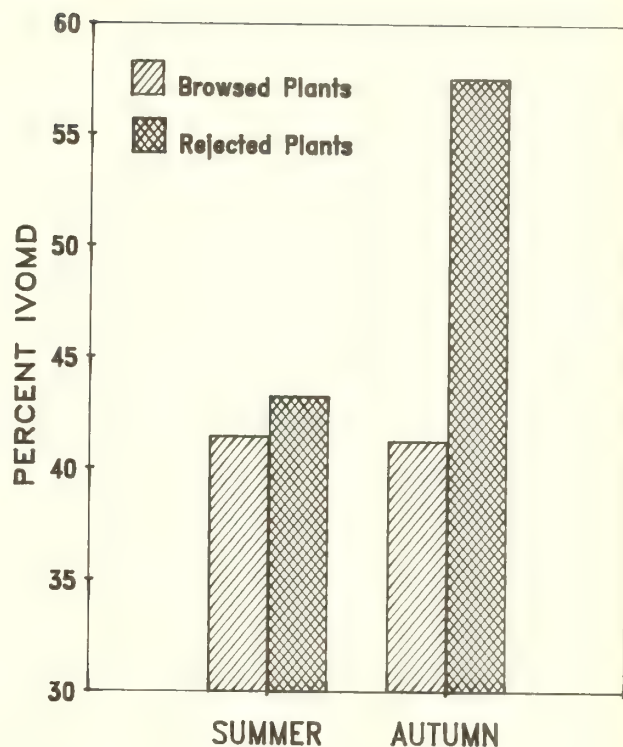


Figure 5.--Percent in vitro organic matter digestibility (IVOMD) of browsed and rejected whole plants during summer and autumn, 1983 (LSD_{.05} = 5.0).

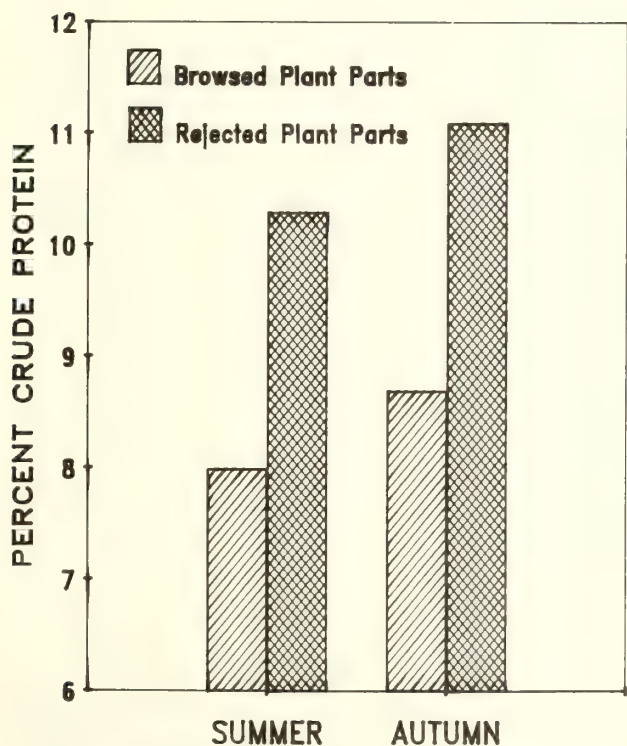


Figure 4.--Percent crude protein of browsed and rejected plant parts during summer and autumn, 1983 (LSD_{.05} = 0.66).

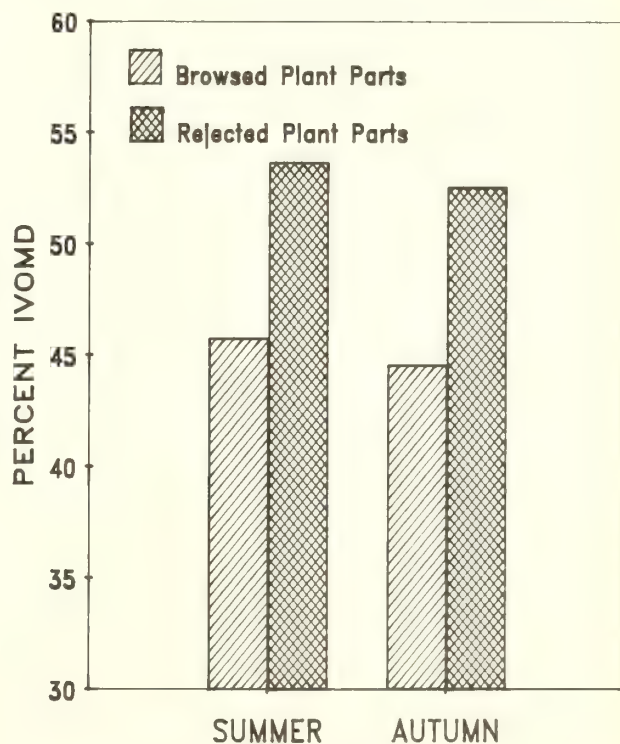


Figure 6.--Percent in vitro organic matter digestibility (IVOMD) of browsed and rejected plant parts during summer and autumn, 1983 (LSD_{.05} = 5.0).



Figure 7.--An example of a preferred older sagebrush plant (left) and a rejected sagebrush plant (right).

lower digestibility and crude protein content of older growth. They concluded that a higher concentration of tannins or some other secondary metabolite found in current season's growth was the chief factor governing diet selection.

As stated earlier, mean monoterpenoid concentrations were higher for fall whole plants (0.87 percent) than for summer (0.53 percent) (fig. 1). Despite this fall increase, sheep utilized sagebrush more heavily in fall than summer. About half of the individual sagebrush plants received a 50 percent or heavier utilization in summer, while 78 percent of the plants in fall were browsed to this level. In addition, sheep were observed to shift from grasses to sagebrush earlier in fall (day 3) than in summer (day 5). During both trials, sheep consumed all the available herbaceous material, including club mosses (*Selaginella* spp.), before browsing sagebrush. Sheep consumed the grasses more quickly in fall than summer, leaving no alternative forage source except sagebrush. Sheehy and Windward (1981) reported that during a palatability trial comparing seven taxa of sagebrush, including *Artemisia tridentata* ssp. *tridentata*, sheep had to be induced to browse sagebrush by removal of other food sources.

The crude protein content of the diet generally increased during the course of both trials (fig. 8). As sheep switched from grasses to shrubs, dietary crude protein content would be expected to increase because shrubs contain higher crude protein levels than mature grasses (Narjisse 1981). Dietary crude protein levels were also higher in fall than in summer. This increase

can be attributed to: (a) the earlier switching from grasses to shrubs, and (b) higher levels of crude protein in sagebrush during fall than summer (fig. 3).

The IVOMD of diets were comparable on day 1 in both summer and fall (fig. 9). However, in summer, digestibility of sheep diets fell sharply by day 3 and remained low through day 5. Sheep ate everything possible prior to eating sagebrush and in the process of consuming leaf litter from the ground they consumed substantial amounts of soil. Large quantities of soil in the diet samples may have depressed *in vitro* digestibility values. Digestibility increased

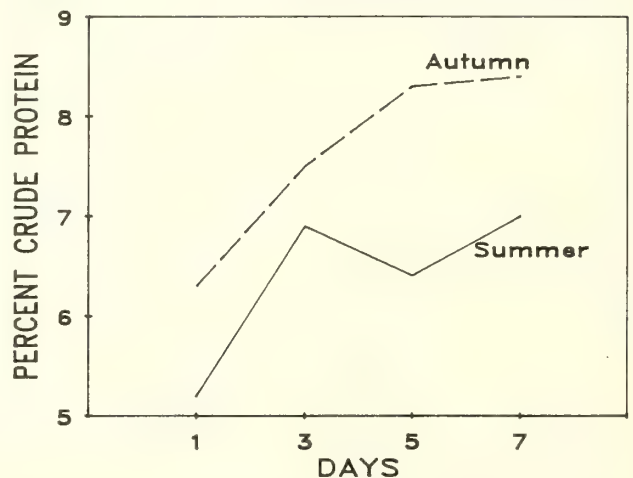


Figure 8.--Comparison of percent crude protein of esophageal fistula extrusa collected from sheep every second day during two seasons (LSD_{.05} = 0.65).

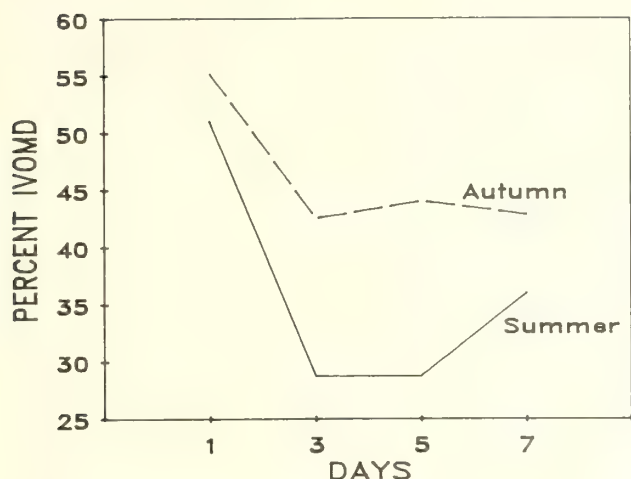


Figure 9.--Comparison of *in vitro* organic matter digestibility of esophageal fistula extrusa collected from sheep every second day during two seasons ($LSD_{.05} = 4.7$).

after sheep began browsing sagebrush (day 7). In fall, digestibility declined on day 3 and remained at that level through day 7. Sheep made the transition from grass to sagebrush earlier, preventing the drastic decline in IVOMD noted in summer. The overall decline in IVOMD can be attributed to the incorporation of woody stem and bark material from sagebrush into sheep diets (Otsyna 1983).

In conclusion, the often-observed positive relationship between dietary selection and proximate chemical constituents (Heady 1964; Fontenot and Blaser 1965; Lindlof and others 1974) did not hold for animals in a big sagebrush community. Sheep generally preferred to browse older growth to current season's growth. Therefore, the strong negative influence of monoterpenoids (or related phytochemicals) appeared to overshadow any positive nutritive considerations. However, Reichardt and others (1984) cautioned that significant correlative data do not necessarily dictate a cause-effect relationship. One or more other phytochemicals that vary in concert with monoterpenoids may have been the causative factor(s). In view of the conflicting reports in the literature relating palatability of sagebrush to monoterpenoid content, more definitive work in this area is needed.

REFERENCES

- Arnold, G. W.; Dudzinski, W. L. Ethology of free-ranging domestic animals. New York: Elsevier Scientific Publishing Co.; 1978.
- Behan, B.; Welch, B. L. Black sagebrush: mule deer winter preference and monoterpenoid content. *J. Range Manage.* 38: 278-279; 1985.
- Bryant, J. P.; Kuropat, P. J. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annu. Rev. Ecol. Syst.* 11: 261-285; 1980.
- Bryant, J. P. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. *Science.* 213: 889-890; 1981.
- Bryant, J. P.; Wieland, G. D.; Reichardt, P. B.; Lewis, V. E.; McCarthy, M.C. Pinosylvins methyl ether deters snowshoe hare feeding on green alder. *Science.* 222: 1023-1025; 1983.
- Cedarleaf, J. D.; Welch, B. L.; Brotherson, J. D. Seasonal variation of monoterpenoids in big sagebrush (*Artemisia tridentata*). *J. Range Manage.* 36: 492-494; 1983.
- Cooper, S. M.; Owen-Smith, N. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia.* 67:142-146; 1985.
- Dietz, D. R.; Nagy, J. G. Mule deer nutrition and plant utilization. In: Workman, G. W.; J. B. Low, eds. *Mule deer decline in the West--A Symposium.* Logan, UT: Utah Agr. Exp. Sta. 1976:71-78.
- Fontenot, J. P.; Balser, R. E. Symposium on factors influencing voluntary intake of herbage by ruminants: selection and intake of grazing animals. *J. Anim. Sci.* 24:1202-1208. 1965.
- Heady, H. F. Palatability of herbage and animal preferences. *J. Range Manage.* 17:76-82; 1964.
- Lindlof, B.; Lindstrom, E.; Pehrson, A. Nutrient content in relation to food preferred by mountain hare. *J. Wildl. Manage.* 38:875-879; 1974.
- Narjisse, H. Acceptability of big sagebrush to sheep and goats. Role of monoterpenes. Logan, UT: Utah State Univ.: 1981. 124 p. Dissertation.
- Neter, J.; Wasserman, W. Applied linear statistical models. Chicago, IL: Richard D. Irwin, Inc. 1974. 842 p.
- Otsyna, R. M. Evaluation of fourwing saltbush and other shrubs as a supplement to crested wheatgrass for sheep in fall and early winter grazing periods. Logan, UT: Utah State Univ. 1983. Dissertation.
- Provenza, F. D.; Malechek, J. C. Diet selection by domestic goats in relation to blackbrush twig chemistry. *J. Applied Ecol.* 21:831-841. 1984.
- Reichardt, P. B.; Bryant, J. P.; Clausen, T. P.; Wieland, G. D. Defense of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia.* 65:58-69; 1984.

- Scholl, J. P.; Kelsey, R. G.; Shafizadeh, F. Involvement of volatile compounds of Artemisia in browse preference by mule deer. Biochem. Syst. Ecol. 5:291-295; 1977.
- Schwartz, C. S.; Regelin, W. L.; Nagy, J. G. Deer preference for juniper forage and volatile oil treated foods. J. Wildl. Manage. 44:114-120; 1980.
- Sheehy, D. P.; Windward, A. H. Relative palatability of seven Artemisia taxa to mule deer and sheep. J. Range Manage. 34:397-399; 1981.
- Tilley, J. M.; Terry, R. A. A two stage technique for the in vitro digestion of forage crops. J. Brit. Grassl. Soc. 18:104; 1963.
- Welch, B. L.; McArthur, E. D. Variation of monoterpenoid content among subspecies and accessions of Artemisia tridentata grown in a uniform garden. J. Range Manage. 34:380-384; 1981.
- Welch, B. L.; McArthur, E. D.; Davis, J. N. Mule deer preference and monoterpenoids (essential oils). J. Range Manage. 36:485-487; 1983.
- Wright, H. A. Response of big sagebrush and three-tip sagebrush to season of clipping. J. Range Manage. 23:20-21; 1970.

PREFERENCE AND DIGESTIBILITY OF THREE BIG SAGEBRUSH SUBSPECIES AND
BLACK SAGEBRUSH AS RELATED TO CRUDE TERPENOID CHEMISTRY

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ABSTRACT: Mule deer (*Odocoileus hemionus hemionus*) demonstrated an order of preference for time spent in five habitat types dominated by four sagebrush (*Artemisia* L.) taxa: basin big sagebrush (*A. tridentata* Nutt. *tridentata*), Wyoming big sagebrush (*A. t. wyomingensis* Beetle and Young), mountain big sagebrush (*A. t. vaseyana* [Rydb.] Beetle), and black sagebrush (*A. nova* Nels.). The taxa were also assigned forage preference ranks based on their winter utilization by mule deer. The in vitro organic matter digestibility of these taxa was determined from samples of intact and extracted (crude terpenoids removed) brush, using rumen fluid inocula from wild mule deer, sheep, and steer. The importance of crude terpenoid chemistry to preference was investigated by identifying and quantifying compounds in the taxa for comparison with preference ranks among taxa.

INTRODUCTION

Sagebrush habitat types are extensive on western rangelands (Beetle 1977); and sagebrush is an important component in the diets of many herbivores (Welch and McArthur 1979). However, when reviewing the literature, it is apparent that there is considerable confusion regarding forage relationships and forage values of the various sagebrush taxa. This is a problem for scientists and rangeland resource managers. Thus, the overall objective of the projects collectively reported in this paper was to relate the forage utility of four sagebrush taxa to their digestibility and unique chemistry.

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STUDY AREA

The area studied and from which sagebrush samples were obtained for laboratory tests is located within the Gallatin National Forest and adjacent to Yellowstone National Park near the town of Gardiner in southwestern Montana. Elevation ranges from 5,300 ft (1 615 m) in the Yellowstone River Valley to 11,000 ft (3 353 m) on the surrounding peaks. The mountains to the south and west create a rain shadow on the study area, making benches and adjacent slopes of the Yellowstone Valley a preferred winter range for large herbivores forced from higher elevations by deep snow. Wintering populations include Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), which spend a large part of their foraging time during the winter on the relatively exposed range dominated by sagebrush.

Annual precipitation at the lower elevations along the Yellowstone River averages 12 inches (300 mm). Most of the winter range receives about 16 inches (400 mm), while the surrounding mountains, snowbound in the winter, receive up to 30 inches (760 mm) (Farnes 1975). About half of the moisture is in the form of snow. The dominant shrub taxa on the area are four sagebrushes (*Artemisia* L. spp.): basin big sagebrush (*A. tridentata* Nutt. ssp. *tridentata*), Wyoming big sagebrush (*A. t.* Nutt. ssp. *wyomingensis* Beetle & Young), mountain big sagebrush (*A. t.* Nutt. ssp. *vaseyana* [Rydb.] B. Boi.), and black sagebrush (*A. nova* A. Nels.). The important grasses, codominant with the shrubs, are bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. & Sm.) and Idaho fescue (*Festuca idahoensis* Elmer) (McNeal 1984).

PREFERRED SAGEBRUSH HABITAT TYPES

Investigations began when McNeal (1984) studied the way mule deer use the Gardiner winter range. He learned that the five shrub habitat types dominated by the four sagebrush taxa were not used by mule deer at an equal rate. This was based on mean pellet-group counts that were believed to represent animal preference for different areas within the winter range.

The high number of deer pellet-groups found within the Wyoming big sagebrush/bluebunch wheatgrass habitat type appeared to show their preference for that type. Sagebrush utilization was heavy in that type, but the area also provided some of the best thermal and security

cover on the winter range in the form of rolling topography and nearby breaks. In addition, nearly all of this habitat type was on south and west exposures, generally without snow accumulation. Intermediate in use were the mountain big sagebrush and black sagebrush habitat types; they had a greater variation in pellet count numbers from one location to another than did the Wyoming big sagebrush type. This variation apparently reflected selective use by deer within these two types with most use found on south or west exposures and on areas near cover. Deer use of the basin big sagebrush habitat type was lowest. Although deer did feed in the basin big sagebrush communities, feeding appeared to be incidental while traveling through the type.

SAGEBRUSH DIGESTIBILITY

A great variety of factors might cause differential use of sagebrush habitat types as observed by McNeal (1984). Examination of forage values of the dominant taxa appeared to be a logical means of relating mule deer preferences to different sagebrush taxa within the winter range. Pursuing this reasoning, we studied the digestibilities of these four sagebrush taxa at three different dates (January 1, February 15, and April 1) with rumen inocula from a domestic sheep and steer as well as a wild mule deer killed on the study area. Concurrently, we measured the change in crude terpenoid content (Kelsey and others 1982) through the winter. In addition, crude terpenoids were extracted from certain sagebrush samples to test the digestibility of sagebrush material not containing these compounds. Investigation of crude terpenoid effects was encouraged by the conjecture of Nagy and others (1964) that monoterpenoids can inhibit deer rumen microbial functions, and the conclusions of research in Utah that rumen microorganisms do not have to adjust to monoterpenoids (Welch and Pederson 1981) and that no relationship could be found between total monoterpenoids and digestibility (Pederson and Welch 1982).

In our investigation (Striby 1985), in vitro organic matter digestibility (IVOMD) was nearly the same for the three inocula sources (mule deer, sheep, and steer). This was true for the different sagebrush taxa, collection dates, and between intact and extracted (crude terpenoids removed) sagebrush materials. The IVOMD of intact sagebrush ranged from a low of 38 percent for the January 1 collection of black sage in mule deer inocula to a high of 63 percent for the February 15 collection of basin big sagebrush, also in mule deer inocula. The IVOMD of extracted sagebrush varied from a low of 44 percent for the February 15 collection of mountain big sagebrush in steer inocula to a high of 76 percent in the April 1 collection of basin big sagebrush in mule deer inocula. Combining all dates, taxa, and inocula sources, the IVOMD of sagebrush averaged 51 percent and 63 percent for intact and extracted sagebrush, respectively. Digestibility of the intact sagebrush taxa

increased in the following order: black sagebrush < mountain big sagebrush < Wyoming big sagebrush < basin big sagebrush. This trend was true regardless of collection date. The order of IVOMD for extracted material differed somewhat from the intact sample; as a rule, the differences among taxa became less significant. Mountain big sagebrush was the taxon with the lowest IVOMD, while black sagebrush, Wyoming big sagebrush, and basin big sagebrush increased in digestibility in that order.

Intact sagebrush taxa had increasing IVOMD through the collection period. This was an inverse relationship to the crude terpenoid level found in the taxa, which decreased over the same time period. For extracted materials, taxa showed few significant changes in digestibility over time, further emphasizing the relationship of crude terpenoids to sagebrush digestion.

Despite our findings regarding sagebrush digestibility and the influence of crude terpenoids on digestion, it was revealing to learn that the order of intact taxon digestibility was not governed strictly by crude terpenoid levels. Basin big sagebrush contained the highest levels of crude terpenoids, yet was the most easily digested. Mountain big sagebrush only exceeded black sagebrush in digestibility yet contained the lowest levels of crude terpenoids followed by black sagebrush and Wyoming big sagebrush. Thus, it became of interest to investigate the preference displayed by browsing mule deer for the four taxa on this range and to subsequently investigate the influence of crude terpenoids on preference.

SAGEBRUSH PREFERENCE

We were able to isolate 32 compounds from the crude terpenoid extract (Personius 1985). Eighteen were identified. The relationship of these compounds to mule deer forage preference on the winter range for the four sagebrush taxa was our main consideration. The order of increasing preference was black sagebrush (least preferred), basin big sagebrush, Wyoming big sagebrush, and mountain big sagebrush (Wambolt, unpublished).

Many of the compounds identified have been tested for biological activity (Tatken and Lewis 1983). Although mule deer were not the subject of these tests, they serve to interpret the possible effects of certain crude terpenoid fractions on mule deer preference. All of the compounds tested were either toxic or irritating, or both, when encountered in sufficient quantities, although the threshold level for mule deer is uncertain. The biological activities of the unknown compounds still remain a question. Some of these are probably toxic or irritating, but there is no way at this time to discern their effects on mule deer preference.

Certain identified biologically active compounds occurred in quantities that seemed both sensible and in sufficiently different concentrations among the sagebrush taxa that correlations to

observed preference appeared meaningful. In addition to being preference indicators, they may be active preference determinants. For example, the amount of methacrolein+ethanol in the three subspecies of big sagebrush had a consistent negative correlation with their preference. Although black sagebrush was the least preferred taxon, and did not contain significant concentrations of methacrolein+ethanol, it did have significantly greater quantities of ρ -cymene. The aforementioned compounds are known to be irritants. The role of certain other compounds in determining preference is less clear. Some were positively correlated to preference; others were less consistent. Compounds that remained unidentified and had a significant correlation to preference provide stimuli for conjecture, but no inference about their possible effect on displayed preference can be made without some knowledge of their biological activity.

SUMMARY AND CONCLUSIONS

Mule deer on the Gardiner winter range displayed a preference among five sagebrush-dominated habitat types. They also displayed a distinct preference for specific sagebrush taxa in their diet. Although many reasons may be responsible for the preference of specific sagebrush habitat types, it is likely that the forage values of the dominant sagebrush taxa play a role. In general, sagebrush taxa were highly digestible throughout the winter browsing period, although high digestibility did not correlate positively to high preference by mule deer. The crude terpenoid chemistry of sagebrush negatively influences digestibility despite the relatively high digestibility of sagebrush with crude terpenoids intact. However, the digestibility of an individual taxon is not directly related to total crude terpenoid content. A distinct preference was displayed for each of the four taxa by mule deer on the winter range and served as a basis for investigating the role of sagebrush compounds on preference. The quantities and biological activities of certain compounds are correlated with the preference demonstrated by mule deer for the four taxa studied.

REFERENCES

- Beetle, A. A. Recognition of *Artemisia* subspecies - a necessity. In: Johnson, K. L., ed. Sixth Wyoming shrub ecology workshop: Proceedings; 1977 May 24-25; Buffalo, WY, Laramie, WY: University of Wyoming; 1977: 35-42.
- Farnes, P. E. Mean annual precipitation for Yellowstone National Park. Bozeman, MT: U.S. Department of Agriculture, Soil Conservation Service; 1975. Unpublished map.
- Kelsey, R. G.; Stephens, J. R.; Shafizadeh, F. The chemical constituents of sagebrush foliage and their isolation. *J. Range Manage.* 35: 617-622; 1982.
- McNeal, A. F. Site characteristics and effect on elk and mule deer use of the Gardiner winter range, Montana. Bozeman, MT: Montana State University; 1984. 133 p. Thesis.
- Nagy, J. G.; Steinhoff, H. W.; Ward, G. M. Effects of essential oils of sagebrush on deer rumen microbial function. *J. Wildl. Manage.* 28: 785-790; 1964.
- Pederson, J. C.; Welch, B. L. Effects of monoterpenoid exposure on ability of rumen inocula to digest a set of forages. *J. Range Manage.* 35: 500-502; 1982.
- Personius, T. L. The influence of crude terpenoid constituents on mule deer preference for big sagebrush and black sagebrush. Bozeman, MT: Montana State University; 1985. 46 p. Thesis.
- Striby, K. D. The in vitro digestibility and utilization of big sagebrush and black sagebrush. Bozeman, MT: Montana State University; 1985. 111 p. Thesis.
- Tatken, R. L.; Lewis, R. J., Sr. Registry of toxic effects of chemical substances, 1981-82 edition, Vol. 1-3. HHS Publication No. 83-107. Washington, DC: U. S. Department of Health and Human Services; 1983.
- Wambolt, C. L. Sagebrush utilization in southwestern Montana. 1983. Unpublished data on file at: Animal and Range Sciences Department, Montana State University, Bozeman, MT.
- Welch, B. L.; McArthur, E. D. Feasibility of improving big sagebrush (*Artemisia tridentata*) for use on mule deer winter ranges. In: Goodin, J. R.; Northington, D. K., eds. International arid lands conference on plant resources: Proceedings; 1979; Lubbock, TX, Lubbock, TX: Texas Tech; 1979: 451-573.
- Welch, B. L.; Pederson, J. C. In vitro digestibility among accessions of big sagebrush by wild mule deer and its relationship to monoterpenoid content. *J. Range Manage.* 34: 497-500; 1981.

SAPONIN EFFECT ON SMALL MAMMAL FORAGE PREFERENCE IN A PLANTING OF

ATRIPLEX CANESCENS

S. C. Sanderson, R. L. Pendleton, E. D. McArthur, and K. T. Harper

ABSTRACT: Accessions of Atriplex canescens transplanted into a newly established common garden were damaged to different degrees by rodents living on the site. The more severely affected plants originated from a small endemic hexaploid race near Grantsville, UT. The remaining collections were two tetraploids and a diploid from other Utah locations. The Grantsville plants were the only ones not bitter to the taste and testing negative in a red blood cell assay for the presence of saponins.

INTRODUCTION

Atriplex canescens has been reported to contain triterpene saponins derived from the aglycone oleanolic acid (Nord and Van Atta 1960). Saponins of this type are not cardiotoxic, but do exert an irritant effect through lysis of cell membranes (Windholz and others 1976; Birk and Peri 1980). Once the glycoside portion of the molecule has been removed in the digestive system it is no longer active, so effects are mostly limited to the throat, or perhaps the lungs in the case of plant dust inhalation. Mammals restricted to saponin-containing diets tend to lose weight, but this may be due to reduced intake (Cheeke 1976).

During the establishment of a garden of Atriplex canescens clones in the spring of 1982, rodents, which are abundant on the site, damaged plants from some sources more than others. Small rodents that are to be expected in this vegetation type include kangaroo rats (Dipodomys), deer mice (Peromyscus), kangaroo mice (Microdipodops), and grasshopper mice (Onychomys) (Fautin 1946; Shelford 1963; Institute for Land Rehabilitation Staff 1978). A. canescens plants from the Grantsville, UT, hexaploid population (Stutz and others 1979), which are nonbitter tasting were especially heavily damaged.

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In preparing the site for planting, native vegetation (Atriplex falcata and Ceratoides lanata) was left undisturbed except in the planted rows. Although the garden had been fenced and the fence lined with partially buried chicken wire to exclude sheep and rabbits, heavy damage was observed on susceptible plants during the spring of planting, and again the following spring in spite of intensive trapping and poisoning. Damage decreased thereafter as plants gained in size. This report documents visible differences in grazing preference by the rodent population.

METHODS

Leaves were dried at 40 °C, ground, and saponin content analyzed by red blood cell assay (Jones and Elliott 1969) using human blood obtained from the American Red Cross. (It was found, however, that drying is better omitted; see Results section). To give a wider range of sensitivity, a single dilution series was used rather than two overlapping series as described by Jones and Elliott (1969). The saponin (1 g or 2 g of dried plant material leached with 23 mL of saline solution) was diluted 1/2, 1/4, ... 1/2¹⁰ (10 tubes) using the following procedure. One milliliter of red blood cell suspension in saline solution (2 percent, v/v) was placed in each of the 10 tubes and 1 mL of the original saponin solution was then added to the first tube. Then half of that mixture from the first tube was transferred to the second tube and half of that mixture to the third, and so on. The solution in tubes where saponin concentration was sufficient to hemolyze the blood cells became a transparent red color, while the solution in unhemolyzed tubes remained translucent red and eventually became clear and colorless as the cells sedimented to the bottom (fig. 1). Titer is referred to as the number of tubes showing hemolysis (tables 1 and 2).

Saponins were also quantified by weight after partial purification. Ten mL aliquots of saponin solution were extracted with three portions (5, 2.5, 2.5 mL) of n-butanol; then n-butanol was evaporated in a tared aluminum foil weighing boat at 50 °C.

A rapid qualitative test for saponins is the foam test (Harborne 1973). The method used in the present study was as follows: 1 g dry weight of ground leaves was mixed with 200 mL water and shaken vigorously. An abundant foam, standing

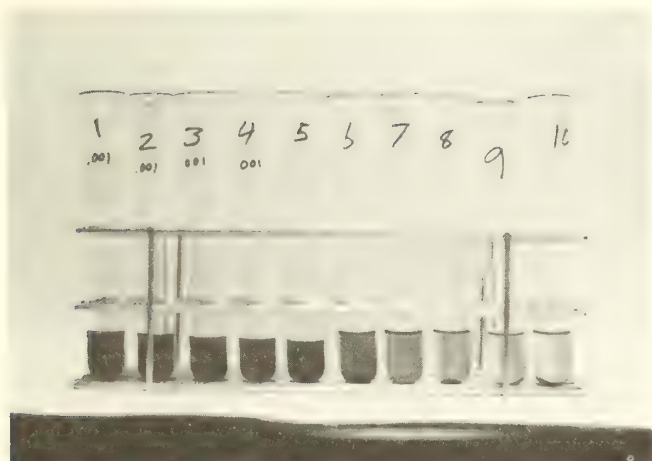


Figure 1.--Hemolysis of blood cells by saponins extracted from *Atriplex canescens*--hemolyzed (left test tubes), partially hemolyzed (tube 6) and unhemolyzed (right test tubes). After standing overnight, cells in the unhemolyzed tubes have sedimented out, leaving a clear solution. Hydrolyzed tubes are colored because of dissolved hemoglobin remaining from disrupted cells.

overnight, was considered a positive test (fig. 2). Human gustatory capabilities are also able to detect *Atriplex* saponins, although the result was usually a rawness of the throat that persisted all day. It was somewhat helpful to wash the mouth copiously with water after performing a test and avoid contact of plant juices with the throat. A small handful of leaves was chewed for 1-2 min, and if the sample contained saponin, a strong bitter taste gradually became apparent.

Table 1.--Saponin content of native *A. falcata* and garden grown *A. canescens* plants of three origins, by erythrocyte assay, from 1 g leaf samples. Plant of origins belonging to separate SNK groupings were statistically different

Origin or species	n	Mean saponin titer	SNK grouping
<i>A. falcata</i>	9	5.89	A
Kingston Canyon	10	4.05	B
Spanish Fork	15	3.80	B
Grantsville	8	0	C

Samples for laboratory analysis were collected from the Rush Valley garden and also from natural populations at Grantsville and Spanish Fork. Rodent damage was recorded the second spring. Plants (10 clones of each) were scored for the presence of chewing damage and the number of plants damaged was converted to a percentage. Percents were arc-sine transformed and treated by one-way analysis of variance followed by the Student Neuman-Keuls multiple mean comparison test (GLM procedure, SAS program for personal computers, Joyner 1985).

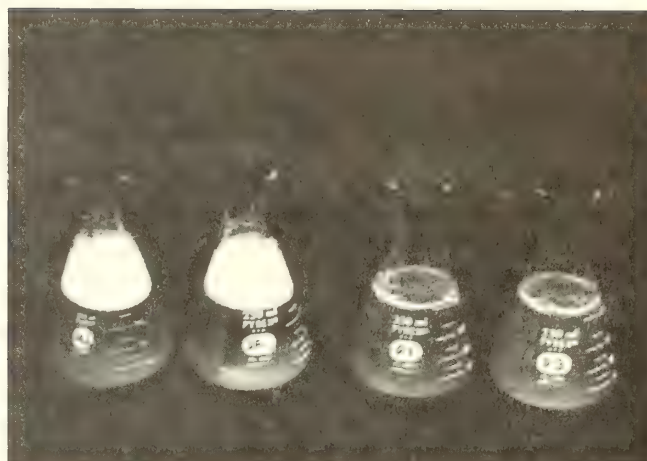


Figure 2.--Positive persistence foam test (two left flasks) in contrast to negative tests (two right flasks). The left flasks contain ground leaves from Spanish Fork *Atriplex canescens*; the right flasks contain leaves from the Grantsville *A. canescens* accession.

Controlled feeding trials were run using a kangaroo rat (*Dipodomys ordi*, male) captured at the Rush Valley site. After capture the animal was fed Hartz Mountain guinea pig pellets (containing primarily alfalfa and soybean meal).

Table 2.--Saponin content of native *A. canescens* from Grantsville and Spanish Fork, by extract weight, foam test, and erythrocyte assay from 2 g leaf samples

Location	n	Mean extract weight, mg	Foam test mode	Mean saponin titer
Spanish Fork	15	81	positive	8.2
Grantsville	15	56	negative	.6

Saponins for feeding trials were obtained from plants of the Spanish Fork *A. canescens* population. Branches were harvested in the month of December and oven dried at 35 °C, and a total of 684 g dry weight of leaves was obtained. These were ground and extracted with 5 gal of 5 percent acetic acid; the acetic acid solution was in turn extracted with n-butanol. The butanol extract was reduced by azeotropic vacuum evaporation and saponin was precipitated from the concentrated solution by removal of dissolved water by azeotropic evaporation. Phenolic impurities were removed by repeated precipitation using this method or the addition of acetone. Twenty-five grams of relatively pure saponins were obtained (as an off-white, chalky solid) and smaller additional amounts appeared to be present in impure fractions, representing a yield of about 3.6 percent or more of the leaf dry weight.

One gram of the final saponin preparation was applied to 49 g of guinea pig food pellets,

either as an alcohol slurry or in water, and the treated pellets were dried under a vacuum. Saponin was incorporated better into the pellet using water, but the pellets were more susceptible to disaggregation if left in water for too long a time. Controls consisted of pellets wetted with water or alcohol and vacuum dried.

RESULTS

Strong statistical documentation was obtained of differences in grazing preference among accessions of A. canescens in the garden (table 3).

Table 3.--Rodent grazing data from the Rush Valley garden of four accessions of A. canescens. "Damage score" is the percentage of plants grazed, arcsine transformed

Origin	n	Mean damage score	SNK grouping
Jericho	11	1.7	A
Spanish Fork	11	4.7	A
Kingston Canyon	11	16.8	B
Grantsville	11	68.0	C

Evidence that this preference was related to saponin content was obtained by measurement of saponins for these accessions. Plants of the Grantsville accession for the most part evidenced no detectable saponins (tables 1 and 2). However, out of 15 plants collected in the field at the Grantsville location (table 2), one plant, perhaps an alien from another A. canescens race, did have a high saponin concentration and a second plant showed a trace. Extract weights shown in table 2 likely consisted of a large amount of phenolic material in addition to saponins.

The accessions in the Rush Valley garden had differing saponin levels but Atriplex falcata growing between the rows tested higher for saponins than any of the A. canescens populations, except inferentially that from the Jericho sand dunes. Although it might be utilized by livestock (Stutz and others 1975), the Jericho accession was grazed least of any A. canescens populations by rodents. However, it was not directly tested for saponins because of early mortality and disappearance from the garden, apparently due to drought sensitivity.

A marked difference is evident between the results of table 1 and 2 with respect to the Spanish Fork accession. In table 1 a mean saponin titer of 3.8 was measured; in table 2 the comparable value was 8.2. This result was partly due to the use of only 1 g of leaf tissue for the measurements in table 1 while in table 2, 2 g were used. Nevertheless each additional titer unit represents a doubling of the initial saponin concentration [conc. = $2^{(n-1)}$], neglecting erythrocyte concentration, so that an eightfold increase in hemolytic power remains unexplained. The collections for the two tables were both made

during the winter and plants seemed in a comparable state of health. However, in the processing, the samples of table 2 were inadvertently overheated in the drying oven to the point that their color was changed somewhat. Myer and Cheeke (1975) found that alfalfa, which contains a type of saponin, became much less palatable to rats when heated during drying. These variations probably result from incomplete cleavage of the inactive saponin precursor by milder treatments (Domon and Hostettmann 1984; Marston and Hostettmann 1985). Drying at mild temperatures might have destroyed the capacity for enzymatic activation of saponins but stronger heating apparently was sufficient to bring about non-enzymatic cleavage of the weak bond of the saponin precursor. In spite of the resulting problem of analysis, which might have been avoided by using fresh rather than dried plant material, the two tables remain internally consistent.

Feeding trials with the kangaroo rat easily demonstrated an animal preference for non-saponin treated pellets when the food was presented in excess above amounts consumed (table 4). However, it was found difficult to demonstrate preference using small amounts because all was commonly taken irrespective of saponin content.

Table 4.--Feeding preference of a kangaroo rat from the Rush Valley site for control versus saponin treated alfalfa pellets

Treatment	n	Mean pct. taken	Std. dev.
Control	4	.9979	.0024
Saponin	4	.1450	.1330

T for unequal variances = 12.8253
df = 3, p = 0.001

DISCUSSION

Although native vegetation, chiefly Ceratoides lanata and Atriplex falcata, of the Rush Valley garden had been mechanically disturbed only in the planting rows, it was adversely affected the first two springs, perhaps by weather or pathogens, to the extent that A. falcata seemed unhealthy and Ceratoides appeared nearly dead. The same was true of areas outside of the garden. As a result a partial food scarcity may have occurred, tending to focus herbivore activities on the newly placed transplants. Fautin (1946) and Shelford (1963) reported that kangaroo rats eat Atriplex confertifolia and A. tridentata (A. nuttallii) leaves, and in spite of the poor conditions of A. falcata, this species was probably abundant enough to be a good food source if it had been sufficiently palatable. The observed differences between A. canescens and A. falcata saponin concentrations (table 1) were probably responsible for the A. canescens transplants being grazed preferentially.

Measurements of saponin content of A. canescens plants showed that a sharp difference existed among the accessions, which is suggested to have influenced herbivore preference. This hypothesis is supported by the response of a captive kangaroo rat to the addition of saponin to commercial food pellets. It may be noted that alfalfa, which formed a major part of the pellets, may contain as much saponin as the Atriplex species examined. However, because of the low reported hemolytic activity of alfalfa (Jones and Elliott 1969) compared with that observed for Atriplex, alfalfa saponin could be expected to produce little aversion in this species of animal. Hence it is not surprising that a clear discrimination was possible on the basis of added Atriplex saponins (table 4).

An attempt was made to demonstrate a feeding preference of the captive kangaroo rat for fresh A. canescens vegetation on the basis of saponin content. However, this was unsuccessful because stems were often gnawed and consumed in preference to leaves. Stems of A. canescens were found to be nonbitter, but splintery. While gnawed off branches of Ceratoides were frequently observed at the site in Rush Valley, Atriplex falcata and A. canescens stems were apparently not gnawed. Perhaps an appetite for stems can be readily satisfied in nature without resorting to those of Atriplex.

Knowledge of variation in saponin levels among A. canescens populations documents an additional character of that species' interpopulational variation to add to those reviewed by McArthur and others (1983) (soil chemistry, ash content, crude protein, stem rooting, palatability, winter hardiness, seed and flower characteristics, growth rate, and chromosome number).

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REFERENCES

Birk, Y.; Peri, I. Saponins. In: Keiner, I. E., ed. Toxic constituents of plant foodstuffs. 2d ed. New York: Academic Press; 1980: 161-182.

Cheeke, P. R. Nutritional and physiological properties of saponins. *Nutr. Rep. Int.* 13: 315-324; 1976.

Domon, B.; Hostettmann, K. New saponins from Phytolacca dodecandra L Herit. *Helv. Chim. Acta* 67: 1310-1315; 1984.

Fautin, R. W. Biotic communities of the northern desert shrub biome in western Utah. *Ecol. Monogr.* 16: 251-310; 1946.

Harborne, J. B. *Phytochemical methods: a guide to modern techniques of plant analysis.* London: Chapman and Hall Ltd.; 1973. 278 p.

Institute for Land Rehabilitation Staff, Utah State University. Rehabilitation of western wildlife habitat: a review. Publ. FWS.OBS-78/86. Washington DC: U.S. Department of the Interior, Fish and Wildlife Service, Biological Services Program; 1978. 238 p.

Jones, M.; Elliott, F. C. Two rapid assays for saponin in individual alfalfa plants. *Crop Sci.* 9: 688-691; 1969.

Joyner, S. P. SAS/STAT guide for personal computers. Version 6 ed. Cary, NC: SAS Institute Inc.; 1985.

Marston, A.; Hostettmann, K. Plant molluscicides. *Phytochemistry* 24: 639-652; 1985.

McArthur, E. D.; Stevens, R.; Blauer, A. C. Growth performance comparisons among 18 accessions of fourwing saltbush (Atriplex canescens) at two sites in central Utah. *J. Range Manage.* 36: 78-81; 1983.

Myer, R. O.; Cheeke, P. R. Utilization of alfalfa meal and alfalfa protein concentrate by rats. *J. Animal Sci.* 40: 500-508; 1975.

Nord, E.; Van Atta, G. R. Saponin--a seed germination inhibitor. *Forest Sci.* 6: 350-353; 1960.

Pedersen, M. W.; Barnes, D. K.; Sorensen, E. L. Effects of low and high saponin selection in alfalfa on agronomic and pest resistance traits and the interrelationships of these traits. *Crop Sci.* 16: 193-199; 1976.

Shelford, V. E. *The ecology of North America.* Urbana, IL: University of Illinois Press; 1963. 610 p.

Stutz, H. C.; Melby, J. M.; Livingston, G. K. Evolutionary studies of Atriplex: a relic gigas diploid population of Atriplex canescens. *Am J. Bot.* 62: 236-245; 1975.

Stutz, H. C.; Pope, C. L.; Sanderson, S. C. Evolutionary studies of Atriplex: adaptive products from the natural hybrid 6n A. tridentata x 4n A. canescens. *Amer. J. Bot.* 66: 1181-1193; 1979.

Windholz, M.; Budavari, S.; Stroumstos, L. Y.; Fertig, M. N. *The Merck Index, an encyclopedia of chemicals and drugs*, 9th edition. Rahway, NJ: Merck and Co.; 1976. 1841 p.

ALKALOIDS AND PALATABILITY OF POISONOUS PLANTS

M. H. Ralphs and J. D. Olsen

ABSTRACT: The alkaloid content of some species (*Phalaris arundinaceae*, *Lupinus* spp., *Crotalaria* spp., and *Senecio* spp.) is inversely related to palatability or has been shown to deter grazing. However, some species (*Delphinium* spp. and *Oxytropis* spp.) high in total alkaloids are apparently palatable to livestock. Other palatability factors appear to override the high alkaloid levels.

INTRODUCTION

C. D. Marsh, principal investigator of the Bureau of Plant Industry for more than 20 years, was an astute observer of poisonous plant/livestock interactions. He made the statement in 1913 that "it is generally recognized that the heaviest losses of livestock from poisonous plants occur in seasons when feed is short. . . . Stock seldom eat poisonous plants by choice, but only when induced or compelled by the scarcity of other food" (Marsh 1913). This concept has been perpetuated in range management literature to the present (Stoddart and Smith 1955; Heady 1975), largely because no one has seen anything drastically contrary to it. Dwyer (1978) addressed a global workshop on poisonous plants 61 years after Marsh's observation and essentially concluded the same thing: "We assume animals do not prefer to graze poisonous plant when given choices." Two exceptions will be mentioned later in this paper. But generally, livestock do not consume poisonous plants in sufficient quantities to cause problems when they have a choice. Most large losses of livestock from poisonous plants result from management mistakes, such as confining hungry livestock on dense concentrations of poisonous plants. Hunger lowers the smell and taste rejection thresholds, thus causing animals to eat plants they normally would avoid (Arnold and Hill 1972).

We can assume then, that there is something in many poisonous plants that livestock find objectionable and deters them from consuming the plants in sufficient quantities to cause harm.

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Alkaloids are the principal toxin in some of the important poisonous plants on rangelands, pastures, and even in cultivated forages. There is some evidence that alkaloids are negatively correlated to palatability for some of these species. Alkaloids are considered to be bitter due to their basic nature. Bate-Smith (1972) made the generalization that bitterness is universally repellent to all animals. However, bitterness is a relative term and may be dependent on the concentration of the alkaloid. Garcia and Hankins (1975) also concluded that natural aversions to bitter substances have been acquired by a wide variety of animal species through natural selection.

There is disagreement, however, on the evolutionary role of alkaloids as defense mechanisms in plants. Waller and Nowacki (1978) suggested that insect herbivory played a large role in the evolution of alkaloids as protective mechanisms in some plant families. However, Robinson (1979) disagreed and stated "sweeping generalities about the protective influence of alkaloids are groundless." He conceded that there are specific cases in which the presence of an alkaloid could influence plant selection by a particular enemy at a particular time. Laycock (1978) reviewed the literature on coevolution of poisonous plants and large herbivores and concluded that there are many examples of the effectiveness of these compounds in deterring grazing. However, he stated that "proof" that they evolved for that purpose is impossible. There is general agreement, though, that if alkaloids in plants are responsible for deterring grazing by large vertebrate herbivores, it is the bitterness or some other factor that renders the plant unpleasant rather than the animal consciously avoiding the toxin (Bate-Smith 1972; Waller and Nowacki 1978; Robinson 1979).

Yet, some poisonous plants with high levels of alkaloids are palatable to livestock. The purpose of this paper is to examine the relationship between palatability and alkaloid content of forage species and poisonous plants consumed by livestock. Specific cases from the literature, published observations, and data from our research will be presented to show cases in which alkaloids deter livestock grazing, as well as instances where livestock select plants that are high in alkaloids.

ALKALOIDS DETER GRAZING

Some forage crops that contain alkaloids present strong evidence of a negative correlation between alkaloid content and palatability.

Reed Canarygrass

Reed canarygrass (Phalaris arundinaceae) is a hardy, high-yielding forage species adapted to upland and poorly drained soils in temperate regions throughout the world. There have been sporadic reports of poor performance by cattle and sheep grazing reed canarygrass pastures, and Phalaris staggers is common in Australia and New Zealand. Several dimethylated tryptamine alkaloids have been isolated from reed canarygrass. They have been shown experimentally to cause "sudden death" syndrome, acute nervous disorders, and the more common symptoms of incoordination of gait and nodding head associated with Phalaris staggers (Marten 1973).

The major criticism of reed canarygrass is its poor palatability. Simons and Marten (1971) conclusively demonstrated a strong negative correlation between total alkaloid concentration (TAC) and palatability. Concentration of individual alkaloids and TAC was determined for 18 clones of reed canarygrass transplanted in a common garden. Palatability ratings were obtained by estimating the proportion of individual plants consumed by sheep given the choice of all the plants in the garden. There had been some discussion that palatability was related to the presence or absence of certain alkaloids, but this research showed that TAC was the major determinant of palatability. TAC ranged from 0.03 percent in the palatable strains to 0.4 percent in unpalatable strains (Hagman and others 1975). This research showed that alkaloids hindered the acceptability of reed canarygrass when a choice was given. Further research revealed that livestock significantly reduced voluntary intake of high alkaloid varieties of reed canarygrass when there was no choice (Marten and others 1976).

Lupine

The Lupinus genus is another example where considerable effort has been made through selective breeding to reduce alkaloid content and thus improve palatability. Quinolizidine alkaloids are the major toxins and teratogens in lupine. Two species of lupine, Lupinus albus in the Mediterranean region and L. matabilis in South America, have been cultivated as grain for over 3,000 years (Gladstones 1970). The seeds traditionally have been debittered by boiling and steeping in running water and then ground as meal or fed to livestock. Gladstones (1970) speculated that the bitterness resulting from alkaloids in seed and foliage has played a large role in protecting the seed source. On the other hand, bitterness in seeds and foliage has probably protected grazing animals by preventing consumption of lethal quantities (Gladstones 1977).

Following World War II, considerable effort was made to breed alkaloid-free or reduced alkaloid "sweet" varieties of lupine for both human and livestock use. Keeler and Gross (1980) analyzed seed from bitter and sweet varieties of lupine used for human consumption from around the world.

They found sweet varieties contained less than 0.10 percent TAC, semisweet varieties contained 0.20 - 0.35 percent TAC, and bitter varieties contained greater than 0.44 percent TAC.

Livestock and other herbivores also discriminate between the high alkaloid bitter varieties and low alkaloid sweet varieties. Blue lupine (L. angustifolius) is a winter annual used as a cover crop in the Southeastern United States. Livestock totally refuse the bitter varieties, but readily graze the sweet varieties (Forbes and others 1961). Lupanine is the principal alkaloid. Bitter varieties contain 0.21 percent lupanine in the leaf and stem as opposed to less than 0.007 percent in the sweet varieties, "Borre" and "Blanco" (Forbes and Burton 1960).

It is difficult to visually distinguish between seeds and growing plants of the sweet variety "Borre" and the original bitter variety. However, cattle rejected pasture of "Borre" sweet lupine when as little as 5-10 percent of the plants were of the bitter variety. Forbes and Beck (1954) developed a biological assay to distinguish bitter from sweet varieties. Thrips fed on pollen of both varieties. When the pollen was exhausted, they went on to attack the foliage of the sweet varieties, but didn't damage the bitter variety. Evidence of thrips damage on foliage was just as accurate as quantification of alkaloids in the plants. Waller and Nowacki (1978) stated that hares grazing L. angustifolius in Poland relished sweet varieties, but left the bitter varieties alone, or if they made a "mistake" and cut the plant off, they left it lying in the field.

Marsh and Clawson (1916) were early investigators of Lupine poisoning of sheep on western ranges. They reported that they had problems getting sheep to eat enough of the plant to cause symptoms of toxicity in pen feeding trials. Seeds were particularly bitter and had to be ground and mixed with bran before sheep would consume them. They concluded that poisoning on the range occurs only when hungry sheep graze the plant and that the alkaloid content is a natural inhibitor.

Davis (1982) reported TAC of several native and improved varieties of lupine ranging from 0.3 to 2.4 percent. The changes in TAC of Lupinus caudatus through its phenological development (fig. 1) is typical of Western United States lupines (Keeler and others 1976). TAC is fairly low at the beginning of growth, rises to a peak prior to flowering, then drops to a low level during the pod stage. Seed TAC range from 2.3 to 9.5 percent. The early vegetative foliage and immature seed pods are palatable to sheep, and correspond to relatively low TAC (fig. 1).

Crotolaria

Crotolaria spp. are used as forage legumes on sandy soils on the coastal plain in the Southeastern United States. Becker and others (1935) evaluated 11 species in palatability trials and found C. spectabilis to be toxic. Cattle did not

LUPINE ALKALOIDS

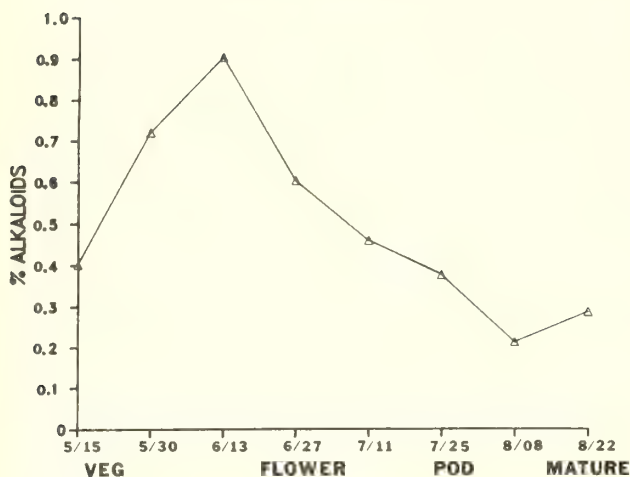


Figure 1.--Percentage of total alkaloids in the total aboveground plant parts of *Lupinus caudatus* through its natural phenological growth stages (Keeler and others 1976).

select *C. spectabilis* in common garden selection trials, and little was eaten as hay or silage when a choice was given. It ranked lowest in palatability. Furthermore, three steers died several weeks following trials in which they were force-fed *C. spectabilis*. Later investigators identified the toxin to be the pyrrolizidine alkaloid, monocrotaline, a hepatotoxin causing chronic liver damage. Animals die weeks to months following the initial insult to the liver (Kingsbury 1964).

Senecio

Senecio spp. also contain pyrrolizidine alkaloids that cause severe problems from hepatotoxicosis throughout the world. Tansy ragwort (*S. jacobaea*) causes severe problems in maritime regions of Australia, New Zealand, Great Britain, the North-western United States, and Canada. Threadleaf groundsel (*S. douglasii* ssp. *longilobus*) and Riddell's groundsel (*S. riddellii*) are common on ranges throughout the Southwest United States. The USDA Forest Service Range Plant Handbook (1937) states that *Senecio* species are seldom grazed except on depleted or over-stocked range. Tansy ragwort is considered quite unpalatable, and cases of poisoning in cattle and horses occur from accidental ingestion while the plant is in the rosette stage and intermixed in low-growing pasture (Muth 1968; Hepworth and Guellette 1979). Threadleaf groundsel is eaten by cattle only when snow covers desirable vegetation or during dry periods (Jones and others 1982). Total pyrrolizidine alkaloid contents for the three species are quite high: Riddell's groundsel 6.4 percent, threadleaf groundsel 2.19 percent, and tansy ragwort 0.2 percent (Johnson and others 1985).

ALKALOIDS THAT DO NOT DETER GRAZING

We have presented some experimental data and several observations of the adverse influence toxic alkaloids have on acceptability of forage species. We now turn to two poisonous plants high in alkaloids, but also palatable to livestock.

Larkspur

The tall larkspurs, dunccecap larkspur (*Delphinium occidentale*) and Barbey larkspur (*D. barbeyi*) are responsible for more cattle deaths on mountain ranges in the Western United States than any other plant (Cronin and Nielsen 1981). On the Manti cattle allotment in central Utah, where accurate records were kept from 1956-1970, average annual cow loss was 4.3 percent; a total of 540 cows lost in a 15-year period (Cronin and Nielsen 1979). Tall larkspur is palatable to both cattle and sheep. However, sheep tolerate four times more larkspur than cattle (Olsen 1978), and the larkspurs in the tall forb vegetative communities on high mountain ranges are considered good sheep forage.

The larkspurs contain several monobasic diterpenoid alkaloids. They present a paradox in that they are really quite high in total alkaloids, yet are readily selected. Figure 2 illustrates the TAC in the plant parts of *D. occidentale* as the plant matures. Observations of cattle grazing the two species indicate that the flowering raceme and immature seed pods are the preferred parts of the plant. Cattle appear to relish the developing seed pods (Knowles 1974; Cronin and Nielsen 1979). These selection patterns correspond to relatively high levels of TAC in the flowering racemes and seed pods.

LARKSPUR ALKALOIDS

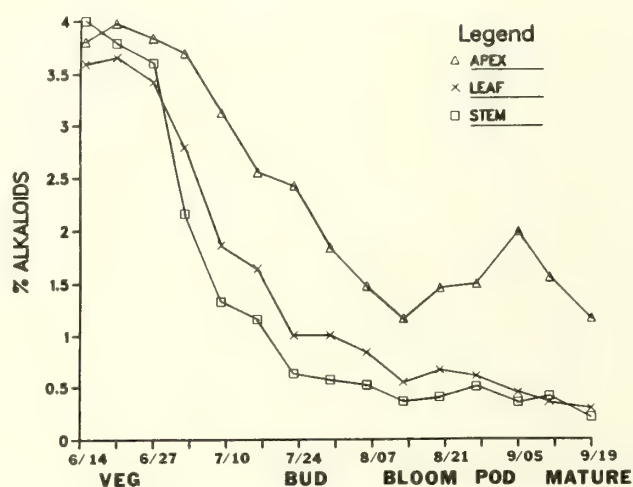


Figure 2.--Percentage of total alkaloids in separate plant parts of *Delphinium occidentale* through its natural phenological growth stages (Kreps 1969).

Williams and Cronin (1963) reported that total alkaloid content in Barbey larkspur increased by 50 and 100 percent following application of 2,4,5-T and Silvex, respectively. In spite of this large increase in TAC, utilization of sprayed plants by cattle increased (Cronin and Nielsen 1972). The plants became more toxic and more palatable, resulting in additional losses. It appears that other palatability factors override the high alkaloid content in tall larkspur.

Locoweed

There are many species of locoweed from the *Astragalus* and *Oxytropis* genera throughout the Western United States. The indolizidine alkaloid, swainsonine, has been identified and implicated as the cause of chronic neurological damage associated with loco poisoning (Molyneux and James 1982). In early studies on loco poisoning, Marsh (1909) observed palatability differences between white locoweed (silky crazyweed; *O. sericea* Nutt.) and wooly locoweed (*A. mollissimus* Torr.). White locoweed was fairly palatable and selected even when grass was abundant, while wooly locoweed was totally rejected when a choice was offered. However, both species appeared equally toxic.

Because of the apparent palatability of white locoweed, grazing trials were conducted to determine how much of the plant cattle consume under natural grazing conditions, which plant parts are selected, and under what environmental and management conditions cattle consume the plant. We found that the reproductive heads were highly preferred (Ralphs and others 1986) and readily consumed even when grass was abundant. Intensive grazing trials, designed to separate the effects of increasing grazing pressure from phenological growth stage of the plant, revealed that steers selected only the immature succulent pods. When other forage was depleted, they began to consume some of the flowers, but no leaves were consumed during the trials even though other forage was depleted (Ralphs, in review). We concluded that the immature succulent pods were the only palatable part of the loco plant.

Technology to quantify swainsonine has not been developed, but the relative concentration, as determined by the intensity of color in the dots on thin-layer chromatography, shows that leaves contain low amounts throughout the season (table 1). Swainsonine content is high in the flower, drops slightly in the immature seed pod, and rises as seeds ripen in the mature pod. It is interesting to note the relationship between swainsonine concentration and nutrient content of loco leaves and heads. Loco leaves are consistently low in swainsonine, but very little leaf is consumed. Loco heads are higher in swainsonine, but also higher in crude protein. Perhaps the higher protein content of the immature pods, other associated nutrients, or palatability factors override the high alkaloid content in cattle preference of pods over leaves.

Table 1.--Relative magnitude of alkaloid concentration and nutrients (percent of dry weight) in white locoweed (Ralphs and others 1986)

Nutrient	Loco part	Bloom	Immature pod	Mature pod	
		Week of grazing season			
		0	2	4	7
Alkaloid	Head	high ¹	moderate	moderate	high
	Leaf	low	low	low	low
Crude Protein	Head	17.3	17.3	17.4	16.4
	Leaf	12.9	12.1	11.8	11.1
Fiber (NDF)	Head	26	38	41	40
	Leaf	32	36	36	36
Water (succulence)	Head	65	60	57	43
	Leaf	69	65	65	51

¹Relative concentration of the alkaloid swainsonine as determined by intensity of color in dots on thin layer chromatography.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

We agree with Robinson (1979) that alkaloids in plants are not universal repellents to herbivory. In some poisonous plants, the presence or high concentration of alkaloids has been shown to deter livestock grazing. For these particular species, poisoning problems result mainly from management mistakes. Hungry animals are confined to areas with high concentrations of the poisonous plant, or other palatable forage is scarce. By knowing the poisonous plants on the range and knowing under what conditions livestock are likely to consume them, a manager can generally avoid serious loss.

Other poisonous plants high in alkaloids are also palatable. Other palatability factors appear to override high alkaloid levels. Further research is necessary to identify these factors and determine their influence on palatability. Further information is also needed on grazing behavior to identify the stages of growth when species are palatable, the amount of the plant an animal must consume to become intoxicated, and the environmental and management conditions under which poisoning is likely to occur. Managing livestock to avoid these conditions may significantly reduce losses. Perhaps aversive conditioning of livestock to avoid these palatable poisonous plants, as described by Provenza and Balph in this proceedings, may be effective in reducing losses. Selective herbicide control may be required to

reduce the concentration of specific poisonous plants if livestock loss is sufficiently high to justify the cost.

REFERENCES

- Arnold, G. W.; Hill, J. L. Chemical factors affecting selection of food plants by ruminants. In: Horborne, J. B., ed. *Phytochemical ecology*. New York: Academic Press; 1972: 71-101.
- Bate-Smith, E. C. Attractions and repellents in higher animals. In: Horborne, J. B., ed. *Phytochemical ecology*. New York: Academic Press; 1972: 45-56.
- Becker, R. B.; Neal, W. M.; Arnold, P. T. D.; Shealy, A. L. A study of the palatability and possible toxicity of 11 species of *Crotolaria*, especially of *C. spectabilis* Roth. *J. Agric. Res.* 50: 911-932; 1935.
- Cronin, E. H.; Nielsen, D. B. Larkspurs and livestock on rangelands of western North America. *Down to Earth*. 37: 11-16; 1981.
- Cronin, E. H.; Nielson, D. B. The ecology and control of rangeland larkspur. *Bull.* 499. Logan, UT: Utah State University, Utah Agricultural Experiment Station; 1979. 34 p.
- Cronin, E. H.; Nielson, D. B. Controlling tall larkspur on snowdrift areas in the subalpine zone. *J. Range Manage.* 25: 213-216; 1972.
- Davis, A. M. The occurrence of anagyrine in a collection of western America lupines. *J. Range Manage.* 35: 81-83; 1982.
- Dwyer, D. D. Impact of poisonous plants on western U.S. grazing systems and livestock operations. In: Keeler, R. F.; VanKampen, K. R.; James, L. F., eds. *Effects of poisonous plants on livestock*. New York: Academic Press; 1978: 13-21.
- Forbes, I.; Beck, E. W. A rapid biological technique for screening blue lupine populations for low-alkaloid plants. *Agron. J.* 46: 528-529; 1954.
- Forbes, I.; Burton, G. W. Blanco blue lupine: a sweet variety insured against bitter mixtures. *Georgia Agric. Res.* 2: 3; 1960.
- Forbes, I.; Marchant, W. H.; Southwell, B. L.; Wells, H. D. Blue lupines for cool season pasture and cover crops in Georgia. Leaflet N.S. 27. Athens, GA: Georgia Agricultural Experiment Station; 1961. 5 p.
- Garcia, J.; Hankins, W. G. The evolution of bitter and the acquisition of toxiphobia. In: Denton, D. A.; Coghlan, J. P. eds. *Olfaction and taste: Proceedings 5th international symposium*; 1974 October; Melbourne, Australia. New York: Academic Press; 1975: 39-45.
- Gladstones, J. S. The narrow-leaved lupin in Western Australia. *Bull.* 3990. Perth, Australia: Western Australia Department of Agriculture; 1977. 39 p.
- Gladstones, J. S. Lupins as crop plants. *Field Crop Abstr.* 23: 123-148; 1970.
- Hagman, J. L.; Marten, G. C.; Hovin, A. W. Alkaloid concentration in plant parts of reed canarygrass of varying maturity. *Crop Sci.* 15: 41-43; 1975.
- Heady, H. F. *Range management*. New York: McGraw-Hill; 1975. 460 p.
- Hepworth, H. N.; Guelette, L. O. Tansy ragwort. Pacific North West Extension Publication PNW-175. Corvallis, OR: Cooperative Extension Service, Oregon State University; 1979. 5 p.
- Johnson, A. E.; Molyneux, R. J.; Merrill, G. B. Chemistry of toxic range plants: variation in pyrrolizidine alkaloid content of *Senecio*, *Amsinckia*, and *Crotalaria* species. *J. Agric. Food Chem.* 33: 50-55; 1985.
- Jones, R. D.; Ueckart, D. N.; Nelson, J. T.; Cox, J. R. Threadleaf groundsel and forage response to herbicides in the Davis Mountains. *Bull.* B-1422. College Station, TX: Texas Agricultural Experiment Station; 1982. 8 p.
- Keeler, R. F.; Gross, R. The total alkaloid and anagyrine contents of some bitter and sweet selections of lupin species used as food. *J. Environ. Pathol. Toxic.* 3: 333-340; 1980.
- Keeler, R. F.; Cronin, E. H.; Shupe, J. L. Lupin alkaloids from teratogenic and non teratogenic lupins. IV. Concentration of total alkaloids, individual major alkaloids and the teratogen anagyrine as a function of plant part and stage of growth and their relationship to crooked calf disease. *J. Toxic Environ. Health.* 1: 899-908; 1976.
- Kingsbury, J. M. *Poisonous plants of the United States and Canada*. Englewood Cliffs, NJ: Prentice-Hall; 1964. 636 p.
- Knowles, K. An evaluation of larkspur poisoning in cattle and the trampling damage that occurs during grazing on a summer range. Moscow, ID: University of Idaho; 1974. 101 p. Thesis.
- Kreps, L. B. The alkaloids of *Delphinium occidentale* S. Wats. Logan, UT: Utah State University; 1969. 65 p. Dissertation.
- Laycock, W. A. Coevolution of poisonous plants and large herbivores on rangelands. *J. Range Manage.* 31: 335-342; 1978.
- Marsh, C. D. Stock poisoning due to scarcity of food. *Farmers' Bull.* 536. Washington, DC: U.S. Department of Agriculture; 1913. 4 p.

- Marsh, C. D. The locoweed disease of the Plains. Farmers' Bull. 112. Washington, DC: U.S. Department of Agriculture; 1909. 130 p.
- Marsh, C. D.; Clawson, A. B. Lupines as poisonous plants. Bull. 405. Washington, DC: U.S. Department of Agriculture; 1916. 45 p.
- Marten, G. C. Alkaloids in reed canarygrass. In: Matches, A. G., ed. Antiquality components of forages. Spec. Publ. 4. Madison, WI: Crop Science Society of America; 1973: 15-31.
- Marten, G. C.; Jordan, R. M.; Hovin, A. W. Biological significance of reed canarygrass alkaloids and associated palatability variation to grazing sheep and cattle. Agron. J. 68: 909-914; 1976.
- Molyneux, R. J.; James, L. F. Loco intoxication: indolizidine alkaloids of spotted locoweed (Astragalus lentiginosus). Science. 216: 190-191; 1982.
- Muth, O. H. Tansy ragwort (Senecio jacobaea): a potential menace to livestock. J. Am. Vet. Med. Assoc. 153: 310-312; 1968.
- Olsen, J. D. Tall larkspur poisoning in cattle and sheep. J. Am. Vet. Med. Assoc. 173: 762-765; 1978.
- Ralphs, M. H. Cattle grazing white locoweed: (2) influence of grazing pressure and palatability associated with phenological growth stage. J. Range Manage. [in review]
- Ralphs, M. H.; James, L. F.; Pfister, J. A. Utilization of white pointloco (Oxytropis sericea Nutt.) by range cattle. J. Range Manage. 39(4): 344-347; 1986.
- Robinson, T. The evolutionary ecology of alkaloids. In: Rosenthal, G. S.; Janzen, D. H., eds. Herbivores--their interaction with secondary plant metabolites. New York: Academic Press; 1979: 413-442.
- Simons, A. B.; Marten, G. C. Relationship of indole alkaloids to palatability of Phalaris arundinaceae L. Agron. J. 63: 915-919; 1971.
- Stoddart, L. A.; Smith, A. W. Range management. 2d ed. New York: McGraw-Hill; 1955. 443 p.
- Waller, G. R.; Nowacki, G. W. Alkaloid biology and metabolism in plants. New York: Plenum Press; 1978. 294 p.
- Williams, M. C.; Cronin, E. H. Effect of Silvex and 2,4,5-T on alkaloid content of tall larkspur. Weeds. 11: 317-319; 1963.
- U.S. Department of Agriculture, Forest Service. Range plant handbook. Washington, DC: U.S. Department of Agriculture, Forest Service; 1937: W 168.

PHYTOCHEMICAL CONSTITUENTS IN A SONORAN DESERT PLANT COMMUNITY

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ABSTRACT: A Sonoran Desert wash woodland plant community at the Philip Boyd Desert Research Center was examined for the distribution of six phytochemical classes. No survey chemical class was represented in more than 7 of the 23 species analyzed. No plant contained more than 3 classes.

INTRODUCTION

The growth and reproduction of plants in an arid desert environment is constrained by a number of environmental factors, primarily the lack of water and nitrogen (Fisher and Turner 1978). Loss of biomass to herbivores represents an additional environmental constraint on these plants. Leaf tissue loss has been proposed as a major barrier to be overcome in such resource limited environments (Janzen 1974) due to the difficulty in replacing lost resources, specifically nitrogen. Phytochemicals have been proposed as one mechanism used by plants to reduce or prevent such losses (Rosenthal and Janzen 1979).

As part of our continuing study of the environmental and biotic parameters of plant growth for a Sonoran Desert wash woodland community, we initiated a survey of six phytochemical classes. Twenty-three species in this community were selected for the survey (table 1). Leaf tissue and stem tissue for the stem photosynthetic plants were analyzed for the presence or absence of the six classes. The survey classes were grouped into nitrogen- and carbon-based defenses. The two nitrogen-based classes were alkaloids and cyanogenic glycosides. The four carbon-based classes were phenolic acids, tannins, saponins, and cardiac glycosides.

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METHODS

Phytochemical Analysis

All plant material was collected in a 2-day period at the University of California's Philip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA. Chemical class analyses were performed on fully mature leaves of all species except Phorodendron (stems, as an aphyllous parasite) and the two stem-photosynthetic plants, Dalea (stems only) and Cercidium (leaves and stems).

Cyanogenic glycosides were measured by macerating fresh plant material in the presence of a Feiger-Angle detection strip. Alkaloid presence was determined by testing acidic hot water extracts of fresh plant material with four reagents (Marne's, Mayer's, Wagner's, and Dragendorff's) (Farnsworth 1966; Wisdom and Smiley 1985). Saponins were assayed by shaking fresh leaf material in deionized water for more than 30 minutes to check for significant foam formation (>2.0 cm). For the remaining three chemical classes, about 1 g of fresh plant material was placed in 30 mL of 80 percent aqueous methanol within 4 hours of collection. After overnight extraction, each sample was filtered for further testing. Ten mL of this extract was evaporated to dryness and resuspended in 20 mL of hot deionized water. Half of this suspension was tested with ferric chloride solution for phenol presence and the other half tested for protein precipitating ability (Wisdom and Smiley 1985). Cardiac glycosides were measured by the application of 80 percent aqueous methanol to filter paper, drying, and spraying the filter paper with 2 percent 2,4-dinitrobenzoic acid solution (Farnsworth 1966).

Phenolic acid presence was determined by a High Performance Liquid Chromatograph (HPLC) system capable of detecting 13 separate acids. Separation of the phenolic acids was performed using a Beckman HPLC (a 421 gradient controller, two 110A pumps, a 504 autosampler, and a Hewlett-Packard 3390A integrator). Solvent A was 100 percent water and solvent B was 100 percent methanol. The flow rate was 2 mL/min for the entire program. The gradient system started with 5 percent solvent B at 0 minutes, ramping linearly to 7 percent, starting at 2 minutes and finishing at 6 minutes. At 12 minutes, the gradient ramped linearly to 25 percent solvent B, ending at 25 minutes. At 30 minutes, the gradient ramped to 100 percent ending at 32 minutes. The gradient stayed isocratic at 100 percent until 36 minutes, the end of the program.

Table 1.--Plant species and growth forms surveyed for the six natural product classes

Plant species	Family	Growth form	Common name
<u>Acacia greggii</u>	Fabaceae	Tree	Gregg Catclaw
<u>Cercidium floridum</u>	Fabaceae	Tree	Blue Paloverde
<u>Chilopsis linearis</u>	Bignoniaceae	Tree	Desert-willow
<u>Dalea schottii</u>	Fabaceae	Tree	Indigo bush
<u>Dalea spinosa</u>	Fabaceae	Tree	Smoke tree
<u>Fouquieria splendens</u>	Fouquieriaceae	Tree	Ocotillo
<u>Hyptis emoryi</u>	Lamiaceae	Tree	Desert lavender
<u>Larrea tridentata</u>	Zygophyllaceae	Tree	Creosote bush
<u>Tamarix aphylla</u>	Tamaricaceae	Tree	Tamarisk
<u>Agave deserti</u>	Agavaceae	Shrub	Century plant
<u>Ambrosia psilostachya</u>	Asteraceae	Shrub	Rag weed
<u>Bebbia juncea</u>	Asteraceae	Shrub	Sweet bush
<u>Beloperone californica</u>	Acanthaceae	Shrub	Chuparosa
<u>Datura discolor</u>	Solanaceae	Shrub	Jimson weed
<u>Hymenoclea salsola</u>	Asteraceae	Shrub	Cheese weed
<u>Krameria grayi</u>	Krameriaceae	Shrub	Krameria
<u>Petalonyx thurberi</u>	Loasaceae	Shrub	Sandpaper plant
<u>Prunus fremontii</u>	Rosaceae	Shrub	Desert apricot
<u>Simmondsia chinensis</u>	Buxaceae	Shrub	Jojoba
<u>Phoradendron californicum</u>	Loranthaceae	Parasite	Mistletoe
<u>Brandegia bigelovii</u>	Cucurbitaceae	Vine	Brandegia
<u>Cucurbita palmata</u>	Cucurbitaceae	Vine	Gourd
<u>Euphorbia micromera</u>	Euphorbiaceae	Herb	Sandmat

RESULTS

Table 2 shows the results of the screening of the 23 plant species for the first 5 chemical classes. A presence/absence (+/-) scoring for cyanogenic glycosides indicated a very weak reaction that developed over a 24 hour period. The +/- reaction for the tannin score resulted from a positive phenol test, but a negative score for protein precipitating ability. No plants yielded a positive score for cardiac glycosides.

Seven of the 13 phenolic acids assayed were detected (table 3). Not present in any of the assayed plants were coumaric, dimethoxybenzoic, gentisic, ferulic, proto-catechuic, syringic, or vanillic acids. Cinnamic acid was the most common phenolic acid found in the surveyed species.

DISCUSSION

Previous chemical class surveys have been confined primarily to a single class among several different communities (Web 1949; Smolenski and others 1972). Other surveys have broadened the number of chemical classes and have included other attributes, such as fiber, but have restricted the surveyed plant species to host choice of a particular herbivore (Janzen and Waterman 1984). Our chemical class study, in contrast, focused on a group of

chemical classes from a particular community of plants as part of our efforts to understand the biological and environmental impacts on the community.

Of the plant species assessed in our survey, none contained cardiac glycosides (table 2). Additionally, no one class of compounds in table 2 was represented in more than 30 percent of the surveyed species. After the phenolic acids, tannins and cyanogenic glycosides had the widest representation, while alkaloids were represented in only a few species (table 2). No species contained more than 3 classes; when present, were always tannins, cyanogenic glycosides, and phenolic acids (tables 2 and 3). Finally, of the 6 classes assayed, only phenolic acids were detected in Tamarix aphylla, Ambrosia psilostachya, Petalonyx thurberi, Cucurbita palmata and Brandegia bigelovii.

Phenolic acids were much more widely represented than any of the other classes (table 3). Cinnamic acid was the dominant phenolic acid present, occurring in over 60 percent of the species surveyed. Salicylic and benzoic acids were the next most common acids (30 and 22 percent), followed by gallic, caffeic, proto-catechinic and p-hydroxybenzoic acids (all less than 15 percent). Dalea spinosa, Beloperone californica, and Agave deserti had no detectable simple phenolic acids present in leaf tissue (table 3).

Table 2.--Results of the presence/absence (+/-) tests for five chemical classes. Species are in the same order as in table 1

Plant species	Cyanogenic glycosides	Alkaloids	Tannins	Saponins	Cardiac Glycosides
<u>Acacia greggii</u>	+	-	+	-	-
<u>Cercidium floridum</u>	+/-	+	-	-	-
<u>Chilopsis linearis</u>	++	-	-	-	-
<u>Dalea schottii</u>	+/-	-	-	-	-
<u>Dalea spinosa</u>	+/-	-	-	-	-
<u>Fouquieria splendens</u>	+/-	-	+	-	-
<u>Hyptis emoryi</u>	+	-	+/-	-	-
<u>Larrea tridentata</u>	-	-	+	-	-
<u>Tamarix aphylla</u>	-	-	-	-	-
<u>Agave deserti</u>	-	-	-	+	-
<u>Ambrosia psilostachya</u>	-	-	-	-	-
<u>Bebbia juncea</u>	+/-	-	-	-	-
<u>Beloperone californica</u>	+/-	-	-	-	-
<u>Datura discolor</u>	+/-	+	-	-	-
<u>Hymenoclea salsola</u>	+	-	-	-	-
<u>Krameria grayi</u>	+	-	+	-	-
<u>Petalonyx thurberi</u>	-	-	-	-	-
<u>Prunus fremontii</u>	+	-	+	-	-
<u>Simmondsia chinensis</u>	+	-	-	-	-
<u>Phoradendron californicum</u>	+/-	-	+	-	-
<u>Brandegia bigelovii</u>	-	-	-	-	-
<u>Cucurbita palmata</u>	-	-	-	-	-
<u>Euphorbia micromera</u>	+/-	-	+	-	-

Table 3.--Distribution of the individual phenolic acids among the species surveyed. Species are in the same order as in table 1

Plant species	p-Hydroxy benzoic	Cinnamic	Gallic	Salicyclic	Caffeic	Benzoic	p-Catechuic
<u>A. greggii</u>		+		+	+		
<u>C. florida</u>		+					
<u>C. Linearis</u>		+				+	+
<u>D. schottii</u>		+					
<u>D. spinosa</u>							
<u>F. splendens</u>				+			
<u>H. emoryi</u>		+					+
<u>L. tridentata</u>	+	+		+	+		
<u>T. aphylla</u>				+			
<u>A. deserti</u>							
<u>A. psilostachya</u>		+					
<u>B. juncea</u>		+				+	
<u>B. californica</u>							
<u>D. discolor</u>			+			+	
<u>H. salsola</u>						+	
<u>K. grayi</u>		+		+			
<u>P. thurberi</u>		+		+		+	
<u>S. chinensis</u>			+				
<u>P. fremontii</u>				+			
<u>P. californicum</u>		+					
<u>B. bigelovii</u>		+	+				
<u>C. palmata</u>		+					
<u>E. micromera</u>		+					

Table 4.--Phytochemical classes not included in the survey, known or suspected in examined plants

Plant species	Additional known or potential classes
<u>Ambrosia psilostachya</u>	Sesquiterpene lactones
<u>Bebbia juncea</u>	Terpenes ¹
<u>Cucurbita palmata</u>	Cucurbitacins ¹
<u>Euphorbia micromera</u>	Latex
<u>Hymenoclea salsola</u>	External flavonoid resins
<u>Hyptis emoryi</u>	Mono- and di-terpenes
<u>Larrea tridentata</u>	External leaf phenolic and lignin resins
<u>Tamarix aphylla</u>	Salt secreting glands

¹Suspected.

While some plants in our survey contained none of the assayed classes, other defense compounds are known or suspected to be present in some of the survey species include lignin, terpene and flavonoid resins, sesquiterpene lactones, cucurbitacins, and latex (table 4). Additional defenses against herbivory appear to be ephemerality of resources (deciduous, permitting only seasonal use) and structural defenses (spines, leaf toughness, and fiber).

This desert washland community appears to be dominated by carbon-based defenses, particularly phenols and terpenes. Such a chemical profile has been described for other nitrogen-limited communities (Janzen 1974; McKey and others 1978). In light of this, a surprising number of species appear to have a limited ability to produce cyanide. This part of our investigation clearly should be reconfirmed. In future studies we plan to study the influence of nitrogen and water on phytochemical class distributions and amounts and how herbivores respond to these plant changes.

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REFERENCES

- Farnsworth, Norman R. Biological and phytochemical screening of plants. *Journal of Pharmaceutical Sciences*. 55(3): 225-276; 1966.
- Fisher, R. A.; Turner, N. C. Plant productivity in the arid and semiarid zones. *Annual Review of Plant Physiology*. 29: 277-317; 1978.
- Janzen, Daniel H. Tropical blackwater rivers, animals, and mast fruiting by Dipterocarpaceae. *Biotropica*. 6(2): 69-103; 1974.
- McKey, Doyle; Waterman, Peter G.; Mbi, C. N.; Gartlan, J. Stephen; Struhsaker, T. T. Phenolic content of vegetation in two African rain forests: ecological implications. *Science*. 202: 61-64; 1978.
- Rosenthal, Gerald A.; Janzen, Daniel H., eds. *Herbivores: their interaction with secondary plant metabolites*. New York: Academic Press; 1979. 718 p.
- Smolenski, S. J.; Silinis, H.; Farnsworth, Norman R. Alkaloid screening. I. *Lloydia*. 35: 1-34; 1972.
- Web, L. J. An Australian phytochemical survey. 1. Alkaloids and cyanogenetic compounds in Queensland plants. *Bulletin* 241. Melbourne, Australia: Commonwealth Scientific and Industrial Research Organization; 1949. 99 p.
- Wisdom, Charles S.; Smiley, John T. Determinants of growth rate on chemically heterogenous host plants by specialist insects. *Biochemical Systematics and Ecology*. 13(3): 305-312; 1985.

JACKRABBIT-SHRUB INTERACTIONS IN THE MOJAVE DESERT

Richard B. Hunter

ABSTRACT: Jackrabbits in the Mojave Desert have been shown to be severely water stressed during dry weather. I postulate that, rather than being absolutely dependent on drinking water, they utilize vegetation growing on the more mesophytic microhabitats. Season, local soil moisture reserves, and local soil fertility were significant variables determining jackrabbit utilization of desert shrubs. With few exceptions, plant species appeared to be of less significance to browsing preference than moisture and nutrient levels.

INTRODUCTION

Jackrabbits (*Lepus californicus*) are the largest herbivorous mammals in the Mojave Desert. Larger herbivores, such as burros, horses, deer, and mountain sheep are restricted to higher altitudes and wetter habitats. Smaller rodents are abundant and diverse (O'Farrell and Emery 1976), and they are adapted to survive on seeds and metabolic water, though some aestivate during summer. Jackrabbits alone are conspicuously dependent on plants for sustenance during the summer-fall-winter dry seasons.

Zoologists and ecologists working on jackrabbits in the Mojave have been concerned with their energy, water, and salt balances (Nagy and others 1976), and their food intake (Hayden 1966b). Botanists have worked primarily on jackrabbit interactions with creosotebush (*Larrea tridentata* (DC.) Cov.) (Boyd 1983; Steinberg and Whitford 1983).

Data from Nagy and others (1976) suggest that jackrabbits cannot survive more than 1 or 2 weeks without drinking water during dry weather. These data conflict with field observations of rabbits far from water sources weeks after rainfall. However, resolution of this conflict can be based on knowledge of the microhabitats utilized by jackrabbits. The water balance studies of Nagy and others (1976) were done with jackrabbits penned in average Mojave Desert conditions, but I propose free animals escape those conditions by consuming vegetation growing on more mesic and fertile microhabitats.

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STUDY AREA AND METHODS

All sites observed were of Mojave Desert vegetation located either on the Nevada Test Site 115 km northwest of Las Vegas, NV or near Daggett, CA. Altitudes ranged from 600 to 1,100 m and rainfall averaged 100-200 mm per year.

Species studied were all native perennials occurring naturally in the areas studied, with the exception of *Salsola paulsenii* Litv., an introduced summer annual. Transplants of *Atriplex Canescens* (Pursh) Nutt., *A. confertifolia* (Torr. & Frem.) Wats., *A. hymenelytra* (Torr.) Wats., *A. polycarpa* (Torr.) Wats., *Ceratoides lanata* (Pursh) Howell, *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Datura innoxia* P. Mill., *Hymenoclea salsola* T. & G., *Larrea tridentata*, *Lepidium fremontii* Wats., *Menodora spinescens* Gray, and *Oryzopsis hymenoides* (R. & S.) Ricker were grown in a glasshouse from locally collected seed. Specimens of *Atriplex canescens*, *A. confertifolia* and *Chrysothamnus nauseosus* (Pallas) Britt. were obtained from Native Plants Incorporated, Salt Lake City, UT. Many other naturally occurring species have been observed, but in either small numbers, few locations, or with ambiguities in determination of browsing animal species.

Browsing estimates were routinely made by imagining a complete symmetric canopy and subjectively estimating the missing volume as a percentage. Comparison of these estimates to dimensional measurements before and after browsing showed the errors were frequently large, but for estimates of >50 percent loss the averages were accurate. Estimates of loss <50 percent averaged 10 percent less than measured losses. Jackrabbit pellet densities were determined by counting pellets in randomly placed 1-m quadrats.

Soil water potentials were determined with thermocouple psychrometers and a dewpoint microvoltmeter. Soil saturation extracts were analyzed with standard techniques (Black and others 1965). Stem water content was determined on sections sealed in scintillation vials immediately after cutting; they were then dried to constant weight over silica gel.

Observations were made in conjunction with research on revegetation of Mojave Desert disturbed areas. Jackrabbits became the major obstacle to restoration of vegetation, and an understanding of their browsing behavior was necessary to efficiently proceed in those efforts.

OBSERVATIONS AND DISCUSSION

In the Mojave Desert, jackrabbit behavior is very similar to that seen in other regions (Hayden 1966a, 1966b; Nagy and others 1976; Shoemaker and others 1976). Long-term population fluctuations have not been measured, but frequencies of field sightings and road kills are quite variable. Annual plants are the preferred foods (Hayden 1966b); shrubs are significantly browsed only in dry seasons. Even in dry weather, the one major summer annual, *Salsola paulsenii*, which is largely restricted to roadsides and disturbed areas, appears to be a major food resource. Thus, on one study site, *S. paulsenii* accounted for 24 of 27 kg/ha of plant material removed (table 1). In spring-time at this same site, pellet densities correlated significantly with annual plant densities ($r = +0.60$, $p < 0.01$), but not significantly with shrub densities ($r = -0.26$).

Table 1.-Estimated jackrabbit browsing on desert plants at Daggett, CA, October 1978

Species	Percent of plants browsed	Percent removed	
		Avg	Median
<i>Ambrosia dumosa</i>	8	8+3	5
<i>Atriplex polycarpa</i>	3	6+2	3
<i>Larrea tridentata</i>	9	18+11	3
<i>Salsola paulsenii</i>	91	21+2	20

Spatial Distribution of Jackrabbit Feeding

The term "desert" is a useful but very broad generalization, and it is necessary to keep in mind that desert resources are spatially variable. There are springs, high altitude woodlands, runoff channels, roadsides, and disturbed areas. Beatley (1976) listed 51 plant species largely restricted to arroyos and disturbed sites. Variability in water resources allows both plant species and jackrabbits to escape from "average" conditions to locations of higher water content. I have evidence that demonstrates higher soil water content, higher plant water content, and enhanced vegetation utilization by jackrabbits for individual disturbed areas.

At one borrow pit study site the rapid growth of shrub seedlings (11 times as fast as control area plants) led me to check soil water status. Soil psychrometers placed on the denuded area showed high water potentials throughout the summer of 1979, while those placed in vegetation 20 m away dried to < -30 bars at all depths (table 2). Soil samples taken in the control vegetation February 19, 1981, had 3.4 ± 0.3 percent water by weight (< 2.0 mm fraction), while samples from the borrow pit averaged 13.5 ± 1.1 percent.

Stem water content in *Larrea tridentata* was measured in samples taken June 27, 1985. On the borrow pit, stems dried to constant weight over

silica gel had 0.46 ± 0.03 g $H_2O/gdw \pm sem$, while those from the control area averaged 0.30 ± 0.03 g/gdw. Steinberger and Whitford (1983) noted a 90 percent increase in browsing incidence on *L. tridentata* when stem water content rose from 35.7 to 38.4 percent.

On this borrow pit jackrabbits appeared to be a major source of shrub seedling mortality. On June 23, 1978 only two of 240 (< 1 percent) marked seedlings had been browsed, while 8 weeks later 152 (63 percent) had been attacked. My interpretation was that until late June rabbits ate annuals and plants growing on this site, but as natural areas dried out (table 2) they began to selectively browse plants growing on the wetter soils of the borrow pit.

At another site, where I followed survival of *Ambrosia dumosa* (Gray) Payne seedlings, I measured browsing damage to *Oryzopsis hymenoides* along a 100 m transect crossing a 43 m disturbed area. Figure 1 shows the marked discontinuity in grazing intensity coinciding with the edges of the disturbance. The rapid growth of *A. dumosa* seedlings on the disturbed section of the transect is evident in figure 2. Figure 3, a and b is a photographic record of the dramatic growth that occurred between January 1984 and June 1985. These differences in growth and browsing incidence can be explained largely on the basis of soil water content; the disturbance was a mere scraping of the surface, and didn't affect soil structure or fertility.

Figure 1 shows that environment can have a major effect on grazing incidence. Another example occurred in February 1981. We transplanted 134 small plants to a site consisting partly of the slope of a dike constructed of compacted subsoils around a waste disposal site and partly of an adjacent flat area whose surface was scraped to facilitate construction. Nine days after transplanting, jackrabbits had breached the fence surrounding the site and browsed many of the transplants. After repairing the fence the degree of damage to each plant was recorded. To our surprise, plants on the dike were less frequently browsed than those on the adjacent scraped area. Of 39 *A. canescens* plants on the dike, 16 (41 percent) were heavily browsed (> 50 percent removed). Of 52 plants on the scraped area, 38 (73 percent) were browsed heavily (table 3). Incidence and degree of damage did not correlate with distance from the hole under the fence, nor with any other obvious spatial factor.

At this time (February) both soils were wet, and growth of annuals and shrubs was limited by temperature. Jackrabbits were obviously selecting plants for some reason other than water availability. In time, another factor became apparent. Growth of plants on the dike was much slower than growth of those on the scraped area (table 3). Psychrometers in the two locations showed higher summer water potentials on the dike (for example, -11 vs. -25 bars on July 29, 1983), contradicting the hypothesis that the dike was drier. Analysis of soil saturation extracts,

Table 2.-Soil water potentials (negative bars) during 1979-80 in a native shrub community and in an adjacent disturbed area without shrubs in Frenchman Flat, NV

Date		Depth of psychrometer placement									
		15 cm		45 cm		90 cm		110 cm		130 cm	
		Bare	Shrubs	Bare	Shrubs	Bare	Shrubs	Bare	Shrubs	Bare	Shrubs
Feb. 8		0	0	1	0	0	0	0	0	0	0
Feb. 16		0	0	0	0	0	0	0	0	0	0
Mar. 29		0	0	0	0	3	0	0	4	0	0
Apr. 12		0	0	0	0	1	0	0	3	0	2
May 7		0	6	1	0	1	2	0	3	0	7
June 1		0	30	2	4	1	0	3	4	1	8
June 7		0	46	0	8	2	4	0	6	2	7
June 14		0	>75	0	10	1	3	0	8	2	17
June 21		0	>69	0	13	3	4	0	9	2	8
July 3		19	>75	1	18	2	5	3	12	0	16
July 9		27	>76	0	25	3	7	0	14	3	14
July 17		>76	>76	0	28	2	12	0	17	3	16
July 25		2	31	0	31	3	20	0	20	0	24
July 31		3	29	1	30	2	24	0	22	1	24
Aug. 7		9	17	0	32	2	28	0	25	3	26
Aug. 14		4	22	0	31	0	28	0	25	1	26
Aug. 21		0	32	0	36	0	31	0	27	2	26
Aug. 28		4	36	0	34	3	31	0	28	2	26
Sept. 4		5	48	0	39	0	33	0	28	2	28
Sept. 11		10	>69	0	38	0	34	0	32	0	--
Sept. 18		30	>73	0	39	2	35	0	32	0	25
Sept. 25		30	>71	0	40	1	35	0	33	0	28
Oct. 9		22	>71	0	40	1	37	0	34	1	30
Oct. 23		14	>64	0	42	2	37	0	33	0	--
Oct. 30		12	--	1	41	0	36	0	34	1	33
Nov. 13		9	--	0	48	2	43	0	35	0	32
Nov. 27		9	>60	0	>59	3	46	0	36	0	32
Dec. 13		7	>59	0	>53	1	42	0	33	0	22
Jan. 8		3	>52	0	>56	0	>52	0	34	0	30
Jan. 22		0	0	0	19	2	>52	0	30	0	16
Feb. 4		0	4	0	0	2	34	0	22	4	15
Feb. 26		0	0	0	--	1	36	0	22	0	15
Mar. 10		0	0	0	0	2	26	0	18	0	13

Table 3.-Size increases (percent) between July 1981 and July 1982, of *Atriplex canescens* transplanted on a dike and adjacent scraped area following jackrabbit browsing in February 1981

Percent browsed	Scraped			Percent increase	Dike		
	N	Survivors			N	Survivors	Percent increase
>90	25	10		4,388	15	2	3,848
50-90	13	10		3,345	1	1	669
<50	2	2		8,563	1	1	332
0	12	11		1,159	22	22	356

however, showed the dike soils to have an EC_{25} of 2.9 ± 1.0 (sem) compared to 1.0 ± 0.4 mMho/cm on the scraped area. Sodium contents were 454 ± 48 and 171 ± 77 mg/L, respectively. Thus, salt content, soil compaction, and undoubtedly several other fertility factors differed in the two soils.

The more fertile soil had higher browsing incidence ($p < 0.01$, χ^2), lower mortality following severe browsing ($p < 0.10$), and more rapid plant growth (table 3). On both soils, plants that survived browsing grew faster than unbrowsed

plants. The simplest explanation for all these observations is that jackrabbits preferentially browsed plants in more fertile soil. Thus, by this hypothesis, plants on the scraped area were more palatable, but because of the better fertility they recovered more easily. An alternative idea, that browsing might stimulate "compensatory" growth, can explain the more rapid growth after browsing, but not the differential browsing incidence and mortality, and is thus a less satisfactory hypothesis.

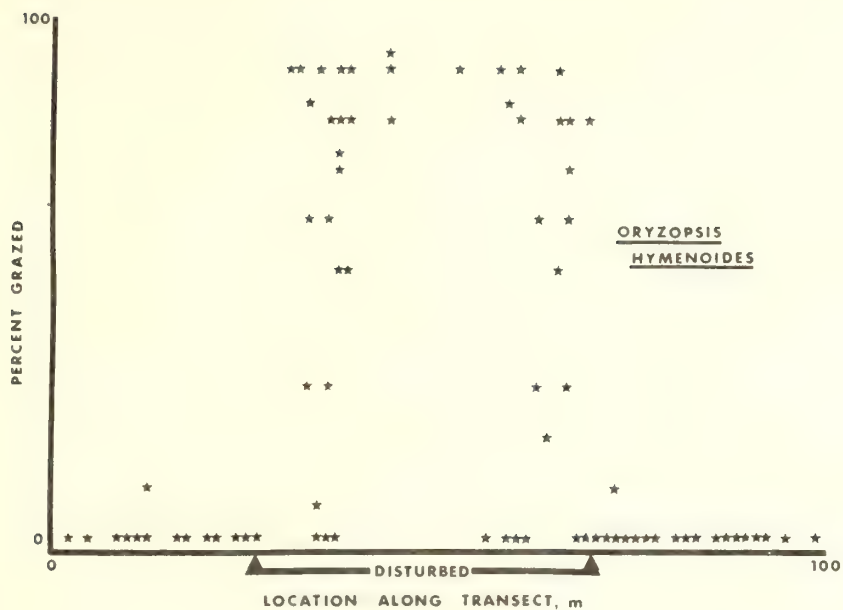


Figure 1.--Grazing incidence and severity along a 100m transect crossing a 42m wide scraped area, January 1984.

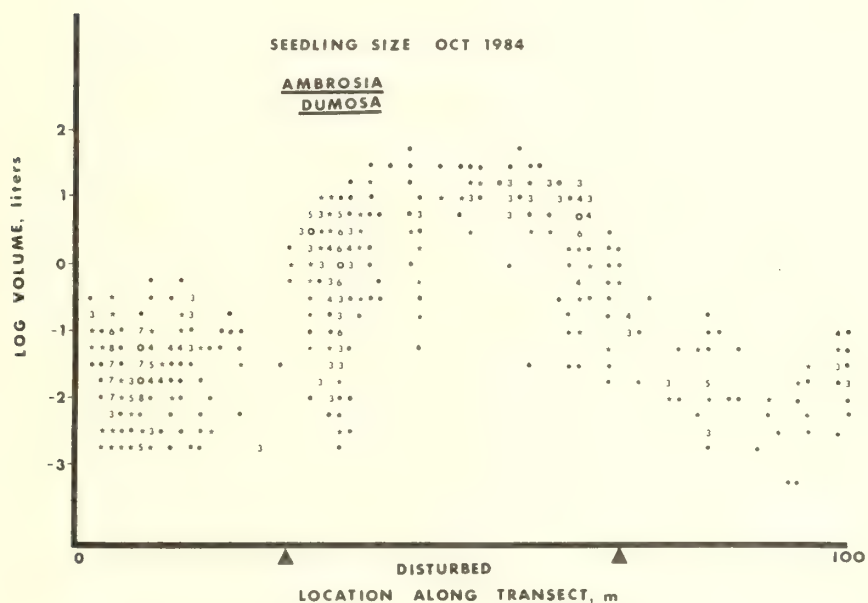


Figure 2.--Sizes of seedlings of *Ambrosia dumosa*, 14 months after germination, along the transect of figure 1. Growth was much faster on the disturbed and heavily grazed section.



A



B

Figure 3.--The scraped area of figures 1 and 2 in A January 1984, and B June 1985, demonstrating the rapid growth of A. dumosa seedlings on the site.

Species Composition of Jackrabbit Diets

One currently favored hypothesis to explain the ubiquity and diversity of "secondary" metabolites" (tannins, alkaloids, nonessential amino acids, etc.) in plants is that they act as feeding deterrents (Harborne 1982). A consequence of that hypothesis is that, where browsing significantly affects a plant community, common species should be unpalatable, and palatable ones rare. Our evidence, however, implied that jackrabbits non-selectively browsed the common species; they avoided only a few rare ones. On the dike, for example, Atriplex canescens (common) was normally reduced to a stub, and Stanleya pinnata (rare) normally suffered only a few bites from a leaf (table 4).

Table 4.-Transplants browsed February 10-19, 1981, by species

Species (N)	Percent not browsed	Percent browsed		
		<50%	<90%	>90%
<u>Atriplex canescens</u> (91)	37	4	15	44
<u>Stanleya pinnata</u> (21)	48	48	4	0
<u>Ambrosia dumosa</u> (7)	57	29	0	14
Others (15)	53	14	6	27

I have transplanted shrubs to quite a number of disturbed sites. The only species I can confidently plant without protection from jackrabbits are Stanleya pinnata, Lepidium fremontii, and Datura innoxia. All three of these species are rare in mature vegetation, though they are more common in washes and disturbed areas. Species that must be fenced to prevent loss include Atriplex confertifolia, A. canescens, A. hymenelytra, A. polycarpa, Ambrosia dumosa, Ceratoides lanata, Chrysothamnus nauseosus, C. viscidiflorus, Hymenoclea salsola, Menodora spinescens, Larrea tridentata, and Oryzopsis hymenoides. These species are all relatively common.

I conclude that species biochemistry evidently holds little importance in jackrabbit-shrub interactions in the Mojave Desert, but soil fertility and moisture content are quite significant. Selection of wetter and more fertile habitats can mitigate, if not obviate, water and calorie stresses in desert jackrabbits in dry seasons. They can then repopulate larger areas in favorable times. Corollaries of these observations are that jackrabbit behavior patterns in mesic areas are also suitable in deserts, and man's disturbance of desert vegetation may significantly increase habitat suitable to jackrabbit survival.

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REFERENCES

- Beatley, Janice C. Vascular plants of the Nevada Test Site and central-southern Nevada: ecologic and geographic distributions. Springfield, VA: National Technical Information Service, U.S. Department of Commerce, 1976, 308 p.
- Black, C. A.; Evans, D. D.; Ensminger, L. E.; White, J. L.; Clark, F. E.; (Eds). Methods of Soil Analysis. Madison, WI: Amer. Soc. Agron.; 1965. 1569 p.
- Boyd, Robert S. Jackrabbit herbivory and creosote bush (Larrea) reproduction. Madrono. 30: 194-195; 1983.
- Harborne, J. B. Introduction to Ecological Biochemistry. New York, Acad. Press; 1982. 278 p.
- Hayden, Page. Seasonal occurrence of jackrabbits of Jackass Flat, Nevada. J. Wildl. Manage. 30(4):835-836; 1966a.
- Hayden, Page. Food habits of black-tailed jackrabbits in southern Nevada. J. Mammal. 47(1): 42-46; 1966b.
- Nagy, K. A.; Shoemaker, V. H.; Costa, W. R. Water, electrolyte, and nitrogen budgets of jackrabbits (Lepus californicus) in the Mojave Desert. Physiol. Zool. 49: 351-363; 1976.
- O'Farrell, Thomas P.; Emery, LaVerne A. Ecology of the Nevada Test Site: a narrative summary and annotated bibliography. Report NVO-167. Springfield, VA: National Technical Information Service, U.S. Department of Commerce, 1976. 249 p.
- Shoemaker, V. H.; Nagy, K. A.; Costa, W. R. The composition, utilization and modification of nutritional resources by the jackrabbit (Lepus californicus) in the Mojave Desert. Res. Memo 73-22. Logan, UT: US/IBP Desert Biome, Utah State University; 1973. 13 p.
- Shoemaker, V. H.; Nagy, K. A.; Costa, W. R. Energy utilization and temperature regulation by jackrabbits (Lepus californicus) in the Mojave Desert. Physiol. Zool. 49: 364-375; 1976.
- Steinberger, Y.; Whitford, W. G. The contribution of shrub pruning by jackrabbits to litter input in a Chihuahuan desert ecosystem. J. Arid Environ. 6: 183-187; 1983.

CHEMICAL COMPONENTS OF CHRYSOTHAMNUS NAUSEOSUS:

A PRELIMINARY EVALUATION

D. Hegerhorst, D. J. Weber, and E. D. McArthur

ABSTRACT: Chrysothamnus nauseosus has a number of subspecies adapted to a wide range of wildland semiarid conditions and can grow from sea level to almost 10,000 ft. They grow on productive as well as saline soils. The species has value in revegetation, as food for wildlife and livestock, for landscaping urban areas, and as a potential source of natural rubber. Gas chromatographic mass spectrometry analysis of the cyclohexane, chloroform, and methanol extracts of C. nauseosus indicated a large range of chemical compounds. Using an MS spectra library search, 70 compounds were identified, many of which may be sources of natural insecticides and fungicides. The significance of these compounds in herbivory has not been determined.

INTRODUCTION

Rabbitbrush (Chrysothamnus) is a dominant shrub in the western semidesert landscape (McArthur 1984). There are 16 species in the genus Chrysothamnus according to Anderson (1986a, 1986b). Three of the Chrysothamnus species are very large groups and form species complexes consisting of a number of subspecies. One of these species complexes is C. nauseosus (rubber rabbitbrush), which occurs in various subspecific forms from the Sonoran to the subalpine life zones and grows from Canada to Mexico and from the Great Plains to the Pacific Ocean. Chrysothamnus nauseosus is a vigorous pioneer plant on disturbed sites such as road sides. It is a shrub that ranges normally from about 12 to 90 inches in height, although populations of rubber rabbitbrush reaching heights of 10 to 12 ft have been observed. The growth pattern of this plant involves erect stems arising from the base, each stem having moderately flexible leaflet branches (McArthur and others 1979; McMinn 1980). In 1923, Hall and Clements (1923) recognized 20 subspecies of C. nauseosus. Some 50 years later, Anderson (1986a, 1986b) recognized 22 subspecies of C. nauseosus, many of them

different from those first recognized by Hall and Clements. The plant grows in the semidesert regions and produces numerous seeds.

Because of the large amount of reproductive structures that are produced, the plant must be effective in its energy production. Chrysothamnus nauseosus exhibits high rates of net photosynthesis (P_n) compared with other woody C_3 photosynthetic pathway species (Davis and others 1985). On both a leaf-area and dry-weight basis, the P_n rate of C. nauseosus is similar to those of the C_4 photosynthetic pathway desert shrubs such as Atriplex canescens. The RuBP and intracellular CO_2 content of rubber rabbitbrush is similar to those found in C_3 photosynthetic pathway crop species (Davis and others 1985). Another interesting property of its photosynthesizing physiology is that the P_n of C. nauseosus is not light saturated at levels equivalent to full sunlight. This may be due to the tomentose vestiture on the leaf's surface that probably shades the chloroplast. In many cases, desert plants possess pubescence as an adaptive means of reducing light absorption. This usually results in a reduced heat load and lower leaf temperature (Ehleringer and Bjorkman 1978). The main effect, however, is that rubber rabbitbrush is capable of maintaining high P_n 's and stomatal conductance in nonstress periods. Thus, it is able to produce dry matter at high rates per unit of biomass.

Chrysothamnus nauseosus is cold-hardy and can tolerate temperature to $-40^\circ F$. It has also been utilized extensively as a revegetation crop (McArthur and others 1979; Hanks and others 1975) because of its ability to grow on disturbed soil and its browse value to livestock and wildlife.

Chrysothamnus nauseosus also attracts interest because it contains natural rubber (Hall and Goodspeed 1919; Ostler and others 1986). The natural rubber was first of interest during World War I when rubber became an important component of the mechanized world. Hall and Goodspeed (1919) published a rather extensive study indicating that over 3 million pounds of rubber were present in the native population of C. nauseosus in the Western United States. Efforts were made during World War I to produce C. nauseosus in the arid west for rubber production. The war ended before commercialization occurred, and interest then dropped. Again during World War II, there was interest in obtaining rubber from both guayule (Parthenium argentatum) and C. nauseosus. After 4 years of work, considerable acreage was near

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commercial rubber production. However, when the war ended, research efforts stopped and plant acquisitions were discarded (Ostler and others 1986). Recently we investigated the rubber and resin content of subspecies of C. nauseosus and found plants with rubber content near 6 percent on a dry-weight basis and resin content up to 16 percent. Ostler and others (1985) obtained similar results in their evaluation of C. nauseosus and found plant populations with 5 percent rubber and 20 percent resin content. Buchannon and others (1978) evaluated desert plant species as potential hydrocarbon crops and found that C. nauseosus contained 11.5 percent hydrocarbons (dry-weight basis). They rated it as having excellent potential as a hydrocarbon crop.

In terms of herbivory and potential significance of the chemicals in the plant, only limited research has been performed. In terms of natural insecticides, Rose and others (1980) found polyacetylenes from C. nauseosus were antifeedants for the Colorado potato beetle. In addition, Maugh and others (1982) found that polyacetylenes from rabbitbrush stimulated plants to produce their own natural insect repellants. Bohlmann and others (1979a, 1979b) found six new labdane acids in C. nauseosus. These may have use as natural insecticides.

METHODS

We investigated more fully the chemical composition of C. nauseosus using gas chromatography and mass spectrometry (MS). The specific epithet, nauseosus, refers to chemical odors of the plant; however, these smells are often pleasant rather than offensive. We selected the subspecies turbinatus because previous analyses determined that it was high in rubber (6 percent) and resin content (16 percent). Samples of C. nauseosus ssp. turbinatus were prepared by harvesting the plant, then grinding the pieces of the stem and leaves in a steel mortar and pestle at liquid nitrogen temperatures. This grinding action resulted in a fine powder that was stored at -20 °C until extracted. Next 20 g of the ground material was extracted first with cyclohexane (three times), then with chloroform (three times), and finally with methanol (three times). These three extracts were concentrated and the mixtures separated by capillary gas chromatography. The compounds in the mixtures were characterized by capillary gas chromatography mass spectrometry. Identification was then made by matching the MS spectra of the compounds analyzed with a library of 78,000 mass spectra (Hewlett-Packard 1985). In those cases in which no high correlation was obtained, the spectra were then analyzed further by the STIRS program (Cornell University), which determines chemical groups and the logical molecular weight of the compound. While many compounds were detected, only the major peaks were identified.

RESULTS AND DISCUSSION

The dominant compounds in the cyclohexane fraction were monoterpenes along with some more complex compounds such as naphthalenes (table 1). The compounds present in the chloroform fraction are shown in table 2. The methanol fraction compounds are shown in table 3. The methanol fraction contained oxygenated polycyclic hydrocarbons such as methylated phenol. Structures of some of the compounds identified are shown in figure 1.

Rubber rabbitbrush is known to attract many insects (McArthur and others 1979; Haws and Bohart 1982). Haws and Bohart (1982), in looking at 18 taxa of range plants located at three outplanting sites in Utah and Wyoming, found an average 51.5 insects per taxon. Rabbitbrush, with 364 insect species, had more than three times as many associated insects as any other plant taxon. Most of the insects detected were beneficial rather than harmful to plant life (Haws 1982). It may be that the diversity of chemical compounds (tables 1-3) and rich insect fauna of rabbitbrush are related. Further research will be necessary to explore this possibility. While we conducted no assays for toxicity or inhibitory actions against insects, some monoterpenes (myrcene, alpha-pinene, delta-3-carene, alpha phellandrene) have been reported to be inhibitory to bark beetles (Rosenthal and Jansen 1979). In addition, high foliar levels of myrcene in Douglas-fir correlate negatively with female and male spruce budworm dry-weight production (Cates and Redak 1984; Cates and others 1983). The significance of those products we identified is not known at this time, but preliminary testing indicated that nematocidal activity is present in the extract of the hydrocarbon fraction as indicated by biological testing done in cooperation with the Ciba Geigy Company (Dumford, personal communication).

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REFERENCES

- Anderson, L. C. An overview of the genus Chrysothamnus (Asteraceae). In: McArthur, E. D.; Welch, B. L., compilers, Proceedings --symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986a: 29-45.

Table 1.--Compounds found in the cyclohexane fraction

Peak number	Name of compound	MW	CAS number	Correlation
A01	Cyclohexanol,3-ethenyl-3-methyl-2-(1-methylethenyl)*	222	35727458	
A02	Beta thujene	136	28634891	0.982
A03	Myrcene	136	123353	.971
A04	Beta bisabolol *	222	15352779	
A05	Nonacosane	408		
A06	C-28 branched chain hydrocarbon	394		
A07	Beta pinene	136	127913	.934
A08	Hentriacontane	436		
A09	C-30 branched chain hydrocarbon	422		
A10	Aristolene	204		.790
A11	Alpha pinene	136	80568	.979
A12	C-29 branched hydrocarbon	408		
A13	Bicyclo[2.2.1]hept-2-ene, 1,7,7-trimethyl-	136	464175	.964
A14	Beta elemene	204	515139	.890
A15	Phenanthrene, 9-methyl-	192	883205	.922
A16	Beta cadinene	204	523477	.987
A17	Alloaromadendrene	204	25246279	.989
A18	Beta caryophyllene	204	87445	.935
A19	Alpha copaene	204	3856255	.987
A20	Gamma cadinene	204	39029419	.995
A21	Alpha thujene	136	2867052	.982
A22	Beta phellandrene	136	555102	.986
A23	Alpha cubebene	204	17699148	.998
A24	Beta cubebene	204	17699148	.975
A25	Alpha gurjunene	204	489407	.995
A26	Alpha elemene	204	5951677	.941
A27	Gamma muurolene	204	30021740	.965
A28	Naphthalene, 1,2,3,4,6,8a-hexahydro-1-isopropyl-4,7-dimethyl-	204	16728997	.971

* Structure probably very similar to this compound. This was determined by a library search and further analyses by Stirs, a computer program to determine structure and probable molecular weight.

Table 2.--Compounds found in the chloroform fraction

Peak number	Name of compound	MW	CAS number	Correlation
B01		204	483761	0.972
B02	Gamma cadinene	204	39029419	.974
B03	1,4-cyclohexadiene,3-ethenyl-1,2-dimethyl-	136	62338572	.951
B04	Alpha muurolene	204	31983229	.946
B05	Bicyclo[4.4.0]dec-1-en,2-isopropyl-5-methyl-9-methylene-	204		.670
B06	Gamma muurolene	204	30021740	.973
B07	Naphthalene,1,2,3,4,6,8a-hexahydro-1,isopropyl-4,7-dimethyl-	204	16728997	.989
B08	1,4,-cyclohexadiene, 3-ethenyl-1,2-dimethyl-	134	62338572	.959
B09	1-methoxy-4-chloro-naphthalene *	192		.580
B10	Nonacosane	408		
B11	Hentriacontane	436		
B12	C28 branched hydrocarbon	394	638368	
B13	C30 branched hydrocarbon	422		
B14	Beta patchoulene	204	514512	.640
B15	Beta pinene	136	127913	.985
B16	Menogene	136	586630	.980
B17	Delta-3-carene	136	13466789	.982
B18	Alpha cubebene	204	17699148	.977

* Structure probably very similar to this compound. This was determined by a library search and further analyses by Stirs, a computer program to determine structure and probable molecular weight.

Table 3.--Compounds found in the methanol fraction

Peak number	Name of compound	MW	CAS number	Correlation
C01	Diocetyl phthalate			0.972
C02	Beta Cadinene	204	523477	.985
C03	Oxacycloheptadec-8-en-2-one	252	123693	.950
C04	(E)-2,3-dimethyl-4-(2',6',6'-trimethyl-1,2'-epoxy clohex-1'-YL)-buta-1,3-diene *	220		.410
C05	Tetradecanonic acid,methyl ester(isomer)	242	124107	.986
C06	Alpha muurolene	204	31983229	.960
C07	Polycyclic hydrocarbon	236		
C08	Polycyclic hydrocarbon	304		
C09	Polycyclic hydrocarbon	264		
C10	Gamma cadinene	204	39029419	.490
C11	Polycyclic hydrocarbon	238		
C12	isomer of C14	235		
C13	Beta cadinene(isomer)	204	523477	.961
C14	1H-indene,2,3-dihydro-1,1,3-trimethyl-3-phenyl- *	236	3910358	.610
C15	Benzeneacetic acid,4-nitro-,4-chlorophenyl ester	291	53218114	.931
C16	Benzene,1,1'-(1,4-dimethyl-1-butene-1,4-diyl)bis-	236	52161543	.936
C17	Polycyclic hydrocarbon	238		
C18	Alpha cubebene	204	17699148	.978
C19	3-cyclohexene-1-ethanol,.alpha.-ethenyl-.alpha.,3-di methyl-6-(1-methylethylidene)- *	220	55780933	.420
C20	similar to C19	220		
C21	Polycyclic hydrocarbon	304		
C22	1,2-benzenedicarboxylic acid, dibutyl ester	278	84742	.988
C23	Decanedioic acid, bis(2-ethylhexyl) ester *	426	122623	.640
C24	Phenol,2,6-bis(1,1-dimethylethyl)-4-methyl-	220	128370	.976
C25	Ethanol,2-[(3-methylphenyl)methoxy]-	166	54411119	.981
C26	silane,tetrafluoro-	104	7783611	.963
C27	Tetradecanonic acid,methyl ester(isomer)	242	124107	.987
C28	1-phenanthrenecarboxylic acid,1,2,3,4,4a,9,10,10a- octahydro-1,4a-dimethyl-7-(1-methylethyl)-,methyl ester,[1R-(1.alpha.,4a.beta.,10a.alpha.)]	314	1235741	.964
C29	4-octanone,2,3-epoxy-2-methyl-	156	17257839	.977
C30	isomer of C22	278		.988
C31	isomer of C22	278		.977

* Structure probably very similar to this compound.
This was determined by a library search and further
analyses by Stirs, a computer program to determine
structure and probable molecular weight.

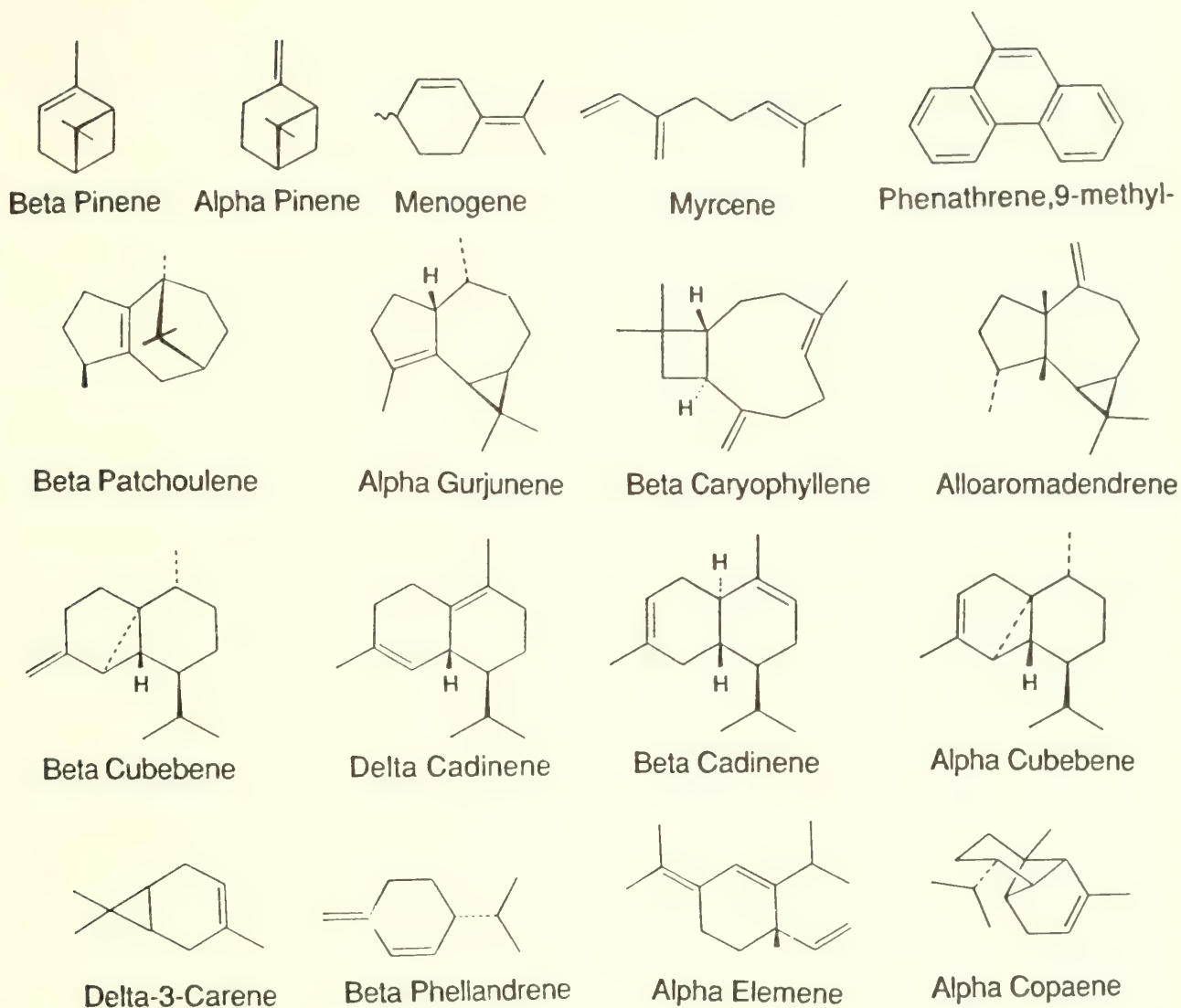


Figure 1.--Structures of some of the compounds identified in Chrysothamnus nauseosus.

- Anderson, L. C. Sympatric subspecies in Chrysothamnus nauseosus. In: McArthur, E. D.; Welch, B. L., compilers. Proceedings--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986b: 98-103.
- Bohlmann, F.; Dutta, L.; Robinson, H.; King, R. M. New labdane derivatives from Chrysothamnus nauseosus. Phytochemistry 18: 1889-1892; 1979a.
- Bohlmann, F.; Zdero, C.; Robinson, H.; King, R. M. New acetylene compounds from Chrysothamnus parryi. Phytochemistry 18: 1519-1522; 1979b.
- Buchannon, R. A.; Cull, I. M.; Otey, F. H.; Russell, C. R. Hydrocarbon and rubber producing crops. Economics of Botany 32: 131-145; 1978.
- Cates, R. G.; Redak, R. Douglas-fir (Pseudotsuga menziesii)--spruce budworm (Choristoneura occidentalis) interactions: the effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. Oecologia 62: 61-67; 1984.
- Cates, R. G.; Redak, R.; Henderson, C. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. Symposium Series No. 208. Washington, DC: American Chemistry Society; 1983: 3-19.
- Davis, T. D.; Sankhla, N.; Anderson, W. R.; Weber, D. J.; Smith, B. N. High rates of photosynthesis in the desert shrub Chrysothamnus nauseosus ssp. albicaulis. Great Basin Naturalist 45: 520-526; 1985.
- Ehleringer, J.; Bjorkman, O. A comparison of photosynthetic characteristics of Encelia species possessing glabrous and pubescent leaves. Plant Physiology 62: 185-190; 1978.
- Hall, H. M.; Clements, F. E. The phylogenetic method in taxonomy: the North American species of Artemisia, Chrysothamnus, and Atriplex. Publication 326. Washington, DC: The Carnegie Institute; 1923. 355 p.
- Hall, H. M.; Goodspeed, T. H. Rubber-plant survey of western North America. Berkeley, CA: University of California; 1919: 159-278.
- Hanks, D. L.; McArthur, E. D.; Plummer, A. P.; Giunta, B. C.; Blauer, A. C. Chromatographic recognition of some palatable and unpalatable subspecies of rubber rabbitbrush in Utah. Journal of Range Management 28: 144-148; 1975.
- Haws, B. A. compiler. An introduction to beneficial and injurious rangeland insects of the western United States. Special Report 23. Logan, UT: Utah State University, Utah Agricultural Experiment Station; 1982. 64 p.
- Haws, B. A.; Bohart, G. E. Families of insects collected in preliminary sweeps in 1979 of 18 species of shrubs at Nephi, Ephraim, and Kemmerer. Logan, UT: Utah State University Department of Biology; 1982. n.p.
- Hewlett-Packard. Computerized mass-spectra library. 1985.
- Maugh, T. H. Exploring plant resistance to insects. Science 216: 722-723; 1982.
- McArthur, E. D. Natural diversity of western range shrubs. In: Cooley, J. L.; Cooley, J. H., eds., Natural diversity in forest ecosystems: proceedings of the workshop; Athens GA: University of Georgia, Institute of Ecology; 1984: 193-209.
- McArthur, E. D.; Blauer, A. C.; Plummer, A. P.; Stevens, R. Characteristics and hybridization of important intermountain shrubs. III. Sunflower family. Research Paper INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1979. 82 p.
- McMinn, H. E. California shrubs. Berkeley, CA: University of California Press, 1980. 663 p.
- Ostler, W. K.; McKell, C. M.; White, S. Chrysothamnus nauseosus: a potential source of natural rubber. In: McArthur, E. D.; Welch, B. L. compilers. Proceedings--symposium on the Biology of Artemisia and Chrysothamnus. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986: 389-394.
- Rose, A. F.; Butt, B. A.; Jermy, T. Polyacetylenes from the rabbitbrush C. nauseosus. Phytochemistry 19: 563-566; 1980.
- Rosenthal, G. A.; Jansen, D. H. Herbivores: their interaction with secondary plant metabolites. New York: Academic Press; 1979. 718 p.

Section 3. Nutrition and Physiology

OVERVIEW OF POISONOUS PLANT-LIVESTOCK INTERACTION IN THE UNITED STATES

Lynn F. James and Michael H. Ralphs

ABSTRACT: Plants that are classified as poisonous are found in most range plant communities. These plants constitute a threat to the livestock grazing these areas. They also provide a challenge to management to devise strategies and procedures to prevent intoxication.

INTRODUCTION

The term "poisonous plant" infers an interaction between a plant containing a toxin and an animal. The presence of poisonous plants on a range or pasture does not mean poisoning will occur. Whether or not poisoning occurs is often dependent on range conditions, weather conditions, management practices, and the species of grazing animal (Sperry and others undated). Nearly all plant communities have plants that contain toxins, and thus are a potential threat to grazing animals. Intoxication occurs if these plants are consumed in sufficient amounts under appropriate conditions. Poisoning presently occurs with sufficient frequency to be a serious problem to livestock production and range management (James 1973).

Poisonous plants are one of the most important causes of economic loss to the livestock industry. Direct losses include death, decreased growth rate, emaciation, abortion, lowered reproductive performance, photosensitization, and birth defects. In addition, indirect costs associated with management such as altered grazing programs, fencing, increased herding costs, losses of forage, supplemental feeding programs, and veterinary fees increase. Poisonous plants on our ranges and pastures also often interfere with the systematic and efficient utilization of forage resources (James 1978).

The dollar loss from deaths and abortions caused by poisonous plants has been estimated to exceed \$199 million annually in the Western United States (Nielsen 1986). If all direct and indirect losses were considered, the total would be much greater. The actual dollar value is difficult to estimate because of insidious losses such as decreased weight gains, increased management costs, and forage losses. Unfortunately, we usually become

alarmed only at large catastrophic losses. Smaller individual losses, or reduced production, have been accepted in the past as part of the costs of grazing rangelands. Because of the present economic crisis in agriculture, ranchers must become more efficient; they cannot afford even a small reduction in production due to poisonous plants.

TOXINS AND TOXICITY

Poisonous plants contain toxins that produce various effects on different classes of livestock. The concentrated efforts of veterinarians, chemists, and animal and range scientists are required to solve the problems caused by poisonous plants.

Intoxication is dependent on dose and rate of consumption. For example, nutrients such as copper, vitamin A, and phosphorus are toxic at high doses. In proper amounts they function as essential nutrients; extremely low levels result in deficiency disease. Many poisonous plants, such as lupine, chokecherry, and larkspur, when grazed under appropriate conditions, are utilized as forages. Lupine is considered, by many sheep producers, an excellent forage and indeed has been utilized extensively on many ranges. Yet lupine has caused the death of many thousands of sheep that ate excessive amounts of the plant.

One must understand the conditions under which these plants can be grazed with relative safety and when they will produce toxic effects in livestock. Some plants such as water hemlock are acutely toxic and cannot be safely grazed in even small amounts. Locoweeds and many forages containing selenium produce chronic intoxication and must be grazed over a period of weeks before intoxication occurs. However, when intoxication is noticed, irreversible damage may already have occurred. These plants should not be grazed at all.

Plants such as bitterweed of the Southwest, Colorado rubberweed, and sneezeweed grow under quite different environmental conditions, yet all contain the same toxin and produce the same signs of intoxication. Intoxication usually occurs under similar management conditions and can be dealt with by the same management strategies. Although these plants can be grazed for short periods of time without serious effects, it is best that they not be grazed at all. Plants that contain low levels of cyanide, nitrate, and oxalate can be grazed in small quantities with little problem. Death occurs when hungry animals are allowed to graze these

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plants rapidly. This usually happens when plants are abundant or in relatively pure stands.

Poisonous plants indigenous to a certain range may not be a problem every year. Environmental conditions influence plant growth and may influence toxicity. Furthermore, plants may vary in toxicity among sites, plant parts, and with stage of growth.

MANAGEMENT IMPLICATIONS

In the early days of grazing in the United States, the availability of free grazing land, the belief that the abundant grass would last forever, lack of knowledge about carrying capacities, and other factors caused serious over-grazing of the range. These attitudes and inexperience resulted in the depletion of much of the natural desirable forage and an increase in less desirable plants, some of which were toxic to livestock.

Much is still unknown about forage preferences of grazing animals. Weather can influence grazing behavior. Drought, heat, cold, and precipitation may induce unusual foraging habits. Under these conditions, unpalatable toxic plants may be consumed in sufficient quantities to cause poisoning on what is normally considered a safe range (Stoddart and others 1949). To minimize losses, the rancher must know the species of poisonous plants on his range, their location and distribution, and conditions that lead to their ingestion.

Some management practices employed by the range livestock industry may be conducive to the poisoning of livestock by plants. For example, lupine is more toxic to cattle than sheep on a unit weight basis, yet thousands of sheep have died from eating this plant while few cattle deaths have been reported. Many sheep have died from halogeton poisoning, yet relatively few cattle have been affected. This plant is about equally poisonous to cattle and sheep. The difference in the number of deaths may have been due to management procedures. Range sheep are kept in large flocks and moved from place to place as deemed necessary by the sheep herder; cattle, however, are left to move freely about a range, limited only by fences and natural barriers. Sheep are watered and provided new forage only by the herder, but cattle are free to search out the necessities of life. Consequently, hungry sheep may be driven through, bedded in, or unloaded from trucks into heavy stands of poisonous plants, and thus exposed to foreign situations. In addition, sheep generally show a preference for shrubs and forbs, which have a higher propensity for accumulating toxins than grasses (James 1973).

Poisoning of livestock under pasture conditions may also occur due to overgrazing and lack of proper attention to the animals. In these situations, as on the large fenced ranges of the Southwest, sheep, like cattle, graze unrestricted; therefore, intoxication from poisonous plants follows a different pattern.

Management activities such as trucking, driving, and penning may cause animals to become hungry and then indiscriminately graze areas that often contain an abundance of poisonous plants. Drought or improper distribution of livestock may result in a deficiency of good forage, which may cause animals to graze poisonous plants. Many poisonous plants are unpalatable and eaten only under stress. On the other hand, some poisonous plants remain green and become relatively more palatable than other plants that have matured and become dry (Everest 1974). Not all poisonous plants are unpalatable, nor are they restricted to overgrazed ranges or pastures. Larkspur, for example, is a climax plant and is readily grazed by livestock (Kingsbury 1964). Whatever the conditions or the poisonous plants, poisoning usually occurs when the animal eats excessive amounts too rapidly.

DISCUSSION

There are three principal methods that might be considered to reduce economic losses caused by poisonous plants: (1) elimination or reduction of the causative plant, (2) treatment of animals, and (3) management strategies to influence the grazing of livestock on ranges and pastures.

The cost of eliminating or markedly reducing populations of poisonous plants where widespread infestations occur must be carefully considered to determine the desirability and feasibility of such an undertaking. Chemical or mechanical treatment of ranges infested with poisonous plants is not always economically feasible, and the terrain may prohibit application of treatments known to be ecologically and economically beneficial.

Medical treatment of livestock poisoned by plants is generally of limited value because of the time interval between intoxication and treatment. Under range conditions, animals cannot be readily observed and often the observations are not frequent enough to detect most problems. In addition, the number of animals poisoned is often large and facilities for handling such animals may be inadequate. Also, there often is no adequate treatment available.

It would appear that the best and most logical approach to the prevention of livestock poisoning by most plants is proper feeding and management. Correct management principles must be applied to the pastures and ranges as well as the livestock. Resource people such as veterinarians, county agents, and land managers can render assistance in identifying the problem and developing management strategies for the prevention of intoxication of livestock by plants.

REFERENCES

- Everest, Selwyn L. Poisonous plants of Australia. Sydney, Australia: Angus & Robertson; 1974. 966 p.

James, L. F. Management as a means of reducing sheep losses due to poisonous plants. In: Proceedings of sheep industry development symposium; profitable range sheep production. 1973 Oct. 23-24; Denver, CO. Denver, CO: Abegg Printing; 1973: 34-37.

James, L. F. Overview of poisonous plant problems in the United States. In: Keeler, R. F.; Van Kampen, K. R.; James, L. F., eds. Effects of poisonous plants on livestock. New York: Academic Press; 1978: 3.

James, L. F. Major toxic plants. California Veterinarian. 37: 21-26; 1983.

Kingsbury, John M. Poisonous plants of the United States and Canada. Engelwood Cliffs, NJ: Prentice Hall; 1964. 626 p.

Nielsen, Darwin B. Economic impact of poisonous plants on the livestock industry. In: Abstracts, Weed Science Society of America 26th annual meeting; 1986 February 5-7. Houston, TX. Champaign, IL: Weed Science Society of America; 1986: 26.

Sperry, O. E.; Dollahite, J. W.; Hoffmann, G. O.; Camp, B. J. Texas plants poisonous to livestock. Bull. 1028. College Station, TX: Texas Agricultural Extension Service; Undated. 53 p.

Stoddart, L. A.; Holmgren, A. H.; Cook C. W. Important poisonous plants of Utah. Special Report No. 2. Logan, UT: Utah Agricultural Experiment Station; 1949: 1-3.

CHEMICAL DEFENSE IN A WOODY PLANT AND THE ROLE
OF DIGESTIVE SYSTEMS OF HERBIVORES

R. Thomas Palo

ABSTRACT: Alcoholic extracts of birch contain the phenolic substances platyphylloside, catechin, and rhododendrol. These phenols are metabolized to a different extent, excreted via different routes and have different physiological effects in hare and domestic rabbit as compared to moose and domestic goat. The same phytochemical may affect digestibility in one type of animal and act parenterally in another.

INTRODUCTION

Diet quality for herbivores is traditionally judged from its content of nutrients and fiber. In recent years attention has been drawn to the possible antinutritional effects of plant secondary metabolites. It has thus been demonstrated that certain polyphenolic compounds may limit availability and digestibility of nutrients (Allison and Osbourn 1970; Swain 1977; Barry and Duncan 1984; Kumar and Singh 1984; Beart and others 1985).

Evidence is also accumulating that soluble cell constituents such as phenolic glucosides, terpenoids, and alkaloids may have significant effects on the nutritive value of a plant (Fairborn 1982; Jung and Fahey 1983; Jung and others 1983; Burritt and others 1984; Lindroth and Batzli 1984; Palo and others 1985; Palo 1985; Risenhoover and others 1985).

The present theory of plant chemical defense against herbivores divides substances into two general categories dependent on their main way of action (Feeny 1976; Cates and Orians 1975; Rhoades 1979). The first category includes substances that depress digestibility and reduce the nutrient availability for the consumer by affecting the digestive process in the gut. The other category contains substances that are readily absorbed in the gastrointestinal tract and act within the body by interfering with various physiological processes.

To what extent and in which way each particular plant substance exerts its biological activity

depends on its molecular size and structure (Rosenthal and Janzen 1979; Scheline 1978; Zucker 1983). In addition, the effectiveness of a defense substance is largely dependent on physiological, behavioral, and ecological adaptations of herbivores to plants (Freeland and Janzen 1974; Janzen 1978; Bernays and others 1980; Rosenthal and others 1977, 1978). The tolerance of xenobiotics by a herbivore is limited by such factors as body size, microsomal activity, feeding strategy, nutritional status, and detoxification capacity (Freeland and Janzen 1974; Fowler 1983; Hanley 1983; Smith and Watkins 1984).

Some thoughts will be presented here about possible differences between the ruminant digestive system compared to the hindgut system of fiber digestion with reference to consumption of Scandinavian birch by moose and hares. Special attention will be given to the excretion pathways of birch phenols by goat, moose, hare, and rabbit. The study is a part of the aim to characterize the chemical defense mechanisms of birch in relation to attack by mammalian herbivores in boreal forest.

MATERIAL AND METHODS

Winter twigs of birch were collected at a clipping point of 1.5 mm and used in different experiments. Feces from goat, moose, rabbit, and hare were collected from caged animals fed twigs as their only feed. The twigs and feces were dried, milled to pass a 1 mm sieve, and then extracted with 95 percent ethanol (EtOH). The extract was filtered through a glass filter and evaporated to dryness. The residue was dissolved in EtOH(1) or water.

The glucosides of the water phase were hydrolyzed with pectinase (D4625, Sigma Co., St. Louis).

Conjugated phenols of the urine were hydrolyzed by treating the urine with sulfatase (S9626, Sigma Co.). The water phase and the urine were then acidified and extracted with ethylacetate (EtOAc). The organic phase was saved, evaporated to dryness, and redissolved in EtOH(2).

Rumen liquor was filtrated and then treated like urine, excluding the enzymatic step.

The samples obtained from step (1) and (2) were purified on sep-pak Silica cartridges (Waters Assor.) and applied on thin-layer chromatography plates (TLC; HPTLC 100 x 100 mm silica gel plates 60, layer thickness 0.25 mm, Merck). The following

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mobile phases were used:

A; chloroform:metanol:water 80:15:1,
B; chloroform:2-butanone:acetic acid 10:7:2 and
C; chloroform:EtOAc 4:1

Spots were visualized by spraying with diazotized sulfanilic acid (Fluka AG, CH. 9470) dissolved in 20 percent sodium carbonate, followed by spraying with 50 percent sulfuric acid.

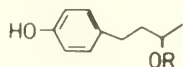
Identification of compounds was made against isolated pure compounds. Substances are presented by their relative front ($R_f \times 100$) values in each mobile phase.

Catechin was obtained from Sigma Co.

RESULTS

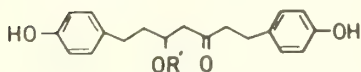
The extract from birch twigs contained three principal phenolic compounds. These are platyphylloside (1,7-di(p-hydroxyphenyl)-heptan-3-one-5ol-5-o-glucoside), rhododendrol (4-(p-hydroxylphenyl)-2-butanol), and catechin (3,5,7,3',4',-flavan-pentol) (fig. 1) (Sannerheim and others, unpubl.). The R_f values in different mobile phases are presented in table 1.

The corresponding analyses of feces, rumen content, and urine show different degrees of metabolism of the substances depending on type of animal and compound (table 2). The TLC chromatograms of feces are identical for moose and goat fed birch. Here one principal metabolite is found. The metabolite was identified by H-NMR data as 1,7-diparahydroxy-phenyl-heptan. Incubation of platyphylloside with rumen liquor of goat showed that it is hydrolyzed and metabolized by rumen microorganisms into this final compound.



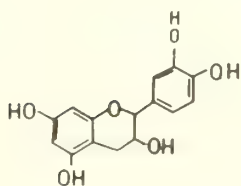
R = Glucose; Rhododendrin

R = H ; Rhododendrol



R' = Glucose; Platyphylloside

R' = H ; Platyphyllone



Catechin

Table 1.-- R_f values for some birch substances in different mobile phases

	$R_f \times 100$		
	A	B	C
Platyphylloside	18	10	0
Platyphyllone	49	86	11
Rhododendrol	53	80	22
1,7-diparahydroxy-phenyl-heptan	59	89	50
Catechin	24	45	0

The analyses of feces from hare and rabbit show that these are identical with each other but differ from goat and moose. Of the studied compounds only rhododendrol is found in the feces of hare and rabbit, but only in small amounts. None of the substances platyphylloside and catechin are found in feces or urine of the animals irrespective of species. Analyses of urine obtained from rabbit and goat fed birch showed that rhododendrol and the final metabolite ($R_f = 59$) are present in both of the animals. Quantitatively more substances are detected in urine of rabbit than in urine from goat.

Catechin cannot be detected on TLC after incubation with rumen inocula from goat or when fed to rabbits. Catechin does not have any measurable effect on in vitro digestion in goats up to a concentration in the feed of 2 percent of the dry weight. On the other hand, the digestibility in vivo in rabbits is reduced by catechin at this concentration but the relative consumption rate is increased (Palo, unpubl. data).

Platyphylloside or one of its metabolites reduces digestibility in ruminants in vitro at a concentration below that naturally occurring in twigs (0.7 percent of dry weight). It also reduces consumption rate (at a concentration of 0.3 percent in rabbits; Palo, unpubl. data).

DISCUSSION

Very limited knowledge exists on the metabolism of phenols or other defensive chemicals in the gut system of herbivores. Some studies have been made on phenolic acids and related monomeric phenols and their metabolism and excretion in ruminants (Martin 1970, 1982; Martin and others 1983). Other studies conducted on rats, rabbits, and guinea pigs include numerous different substances (Scheline 1978). However, the authors do not emphasize differences in digestive system as a factor of importance for the metabolism and excretion of phytochemicals. Furthermore, in the discussion of plant chemical defense theory, herbivores have hitherto been regarded as static in their response to different defense categories (for example, Rhoades 1979). My data imply that differences in excretion pathways and metabolism between different types of animals could be influenced by type of digestive system of the animals.

Figure 1.-- Structural formulas for the studied substances (from Tarasawa 1973, 1984; Haslam 1979).

Table 2.-- Occurrence of some birch substances in excreta of different herbivores. + = major occurrence, - = small amounts, 0 = not detected

	Hare	Rabbit		Moose	Goat		
	feces	feces	urine	feces	feces	rumen	urine
Platyphylloside	0	0	0	0	0	0	0
Platyphyllone	-	-	+	0	0	+	-
Rhododendrol	-	-	-	0	0	+	-
1,7-dipara-hydroxy-phenyl-heptan	0	0	+	+	+	+	-
Catechin	0	0	0	0	0	0	0

In this study, catechin seems to be completely metabolized in the digestive system of both rabbit and goat, but the digestibility was depressed in the former. Scheline (1978) and Harborne (1979) report that microorganisms metabolize catechin to carbon dioxide and a simple phenolic acid. This degradation pattern is common for many flavonoids and in fact all the usual phenolic acids recovered from urine of herbivores seem to originate from bacterial degradation of the feed (Harborne 1979). Furthermore, catechin may spontaneously form di- and trimers which can form complexes with macromolecules (Haslam 1979).

These complexes may be dissolved either in the rumen or in the hindgut. The catechin is then completely metabolized by bacteria. The released macromolecules can be degraded by the rumen microbes, while in the nonruminant they may escape degradation due to a fairly short transit time through the gastro-intestinal tract. This may explain the different effects of catechin in the goat and in the rabbit.

The glucoside platyphylloside is hydrolyzed by the rumen microorganisms to its aglucone platyphyllone and then further metabolized in the rumen to 1,7-dipara-hydroxy-phenyl-heptan. The overall result of these processes is a reduced organic matter digestibility (Palo and others 1985; Sunnerheim and others, unpubl.). The appearance of the final metabolite in the feces of the goat and the moose suggests that it has either not been absorbed or more probably is being reexcreted in the bile. However, part of the platyphyllone apparently escapes degradation and is excreted in the urine.

On the contrary, the final metabolite is excreted only in the urine by rabbits and hares. Probably the hydrophilic platyphylloside passes unchanged down to the large intestine in these animals and then follows the water phase which is forced back into the caecum by the colon separation mechanism and retained (Björnhag 1972). Platyphylloside is then hydrolyzed and further metabolized to platyphyllone and the final metabolite, both of which diffuse through the gut wall and appear in the urine.

The results from studies on catechin and platyphylloside support the idea that anatomical differences in the digestive system affect the metabolism and excretion of secondary plant substances, and more important, how they exert their physiological effects. Catechin has, for instance, no effect in the goat but reduces organic matter digestibility and daily food consumption in the rabbit.

The present results, albeit preliminary, ought to allow the conclusion that one and the same secondary plant substance (or its metabolites) may exert its effect in the intestine of one species and parenterally in another.

The degradation of fibrous material in the rumen determines the rates of passage of food through the digestive tract of ruminants (Van Soest 1982; Demment and others 1985). Hares and rabbits are not to the same extent limited by particle size of food. Consequently, substances depressing digestibility would be of greater importance for the food processing capacity in the ruminant than in the nonruminant herbivore. On the other hand, the latter type of herbivore may be more sensitive to substances that are rapidly absorbed. Presumably, the herbivore will attempt to minimize the intake of certain substances that depress digestibility or that have toxic properties, depending on the particular digestive system of the animal.

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REFERENCES

- Allison, D.W.; Osbourn, D.F. The cellulose-lignin complex in forages and its relationship to forage nutritive value. *J. Agric. Sci. (Camb.)* 74: 23; 1970.
- Barry, T.N.; Duncan, S.J. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. *Br. J. Nutr.* 51: 485-491; 1984.
- Beart, J.E.; Lilley, T.H.; Haslam, E. Plant polyphenols-secondary metabolism and chemical defense: some observations. *Phytochemistry* 24: 33-38; 1985.
- Bernays, E.A.; Chamberlain, D.; McCarthy, P. The differential effects of ingested tannic acid on different species of Acridoidea. *Entomol. Exp. Appl.* 28: 158-166; 1980.
- Björnhag, G. Separation and delay of contents in the rabbit colon. *Swedish J. Agric. Res.* 2: 235-136; 1972.
- Burritt, E.A.; Bittner, A.S.; Street, J.C.; Anderson, M.J. Correlations of phenolic acids and xylose content of cell wall with in vitro dry matter digestibility of three maturing grasses. *J. Dairy Sci.* 67: 1209-1213; 1984.
- Cates, R.; Orians, G.H. Successional status and the palatability of plants to generalize herbivores. *Ecology* 56: 410-418; 1975.
- Demment, M.W.; Van Soest, P.J. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125: 641-672; 1985.
- Fairborn, M.L. Alkaloid affects in vitro dry matter digestibility of *Festuca* and *Bromus* species. *J. Range Manage.* 35: 503-504; 1982.
- Feeny, P. Plant apparency and chemical defense. *Recent Adv. Phytochem.* 10: 1-40; 1976.
- Fowler, M.E. Plant poisoning in free-living wild animals: A review. *J. Wildl. Dis.* 19: 34-43; 1983.
- Freeland, W.J.; Janzen, D.H. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108: 269-289; 1974.
- Hanley, T.A. The nutritional basis for food selection by ungulates. *J. Range Manage.* 35: 145-151; 1982.
- Harborne, J. Flavonoid pigments. In: Rosenthal, G.A.; Janzen, D.H. eds. *Herbivores. Their interactions with secondary plant metabolites.* New York: Acad. Press; 1979; 619-656.
- Haslam, E. Vegetable tannins. In: Swain, T.; Harborne, J.B.; Van Sumere, C. eds. *Biochemistry of plant phenolics.* Recent Adv. *Phytochem.* 12: 475-524; 1979.
- Janzen, D.H. Complications in interpreting the chemical defenses of trees against tropical arboreal plant-eating vertebrates. In: G.G. Montgomery. *The ecology of Arboreal Folivores.* Washington: Smithsonian Institution; 1978; 73-84.
- Jung, H.J.G.; Fahey, G.C. Jr.; Garst, J.E. Simple phenolic monomers of roughages and effects of in vitro fermentation on cell wall phenolics. *J. Anim. Sci.* 57: 1294-1305; 1983.
- Jung, H.J.G.; Fahey, G.C. Nutritional implications of phenolic monomers and lignin: a review. *J. Anim. Sci.* 57: 206-219; 1983.
- Kumar, R.; Singh, M. Tannins: Their adverse role in ruminant nutrition. *J. Agric. Food Chem.* 32: 447-453; 1984.
- Lindroth, R.L.; Batzli, G.O. Plant phenolics as chemical defenses: effects of natural phenolics on survival and growth of prairie voles (*Microtus ochrogaster*). *J. Chem. Ecol.* 10: 229-244; 1984.
- Martin, A.K. urinary aromatic acid excretion by fed and fasted sheep in relation to protein metabolism in the rumen. *Br. J. Nutr.* 30: 251-267; 1970.
- Martin, A.K. The origin of urinary aromatic compounds excreted by ruminants. The metabolism of phenolic compounds to simple phenols. *Br. J. Nutr.* 48: 497-507; 1982.
- Martin, A.K.; Milne, J.A.; Moberly, P. The origin of urinary aromatic compounds excreted by ruminants. The potential use of urine aromatic acid and phenol outputs as a measure of voluntary food intake. *Br. J. Nutr.* 49: 87-99; 1983.
- Palo, R.T. Chemical defense in birch: inhibition of digestibility in ruminants by phenolic extracts. *Oecologia* 68: 10-14; 1985.
- Palo, R.T.; Sunnerheim, K.; Theander, O. Seasonal variation of phenols, crude protein and cell wall content of birch (*Betula pendula* Roth.) in relation to ruminant in vitro digestibility. *Oecologia* 65: 314-318; 1985.
- Rhoades, D.F. Evolution of plant chemical defense against herbivores. In: Rosenthal, G.A.; Janzen, D.H. eds. *Herbivores: their interaction with secondary plant metabolites.* New York: Academic Press; 1979; 4-54.
- Risenhoover, K.L.; Renecker, I.A.; Morgantini, L. Effects of secondary metabolites from balsam poplar and paper birch on cellulose digestion. *J. Range Manage.* 38: 370-372; 1985.
- Rosenthal, G.A.; Janzen, D.H. *Herbivores: their interaction with secondary plant metabolites.* New York: Academic Press; 1979. 718 p.

- Rosenthal, G.A.; Janzen, D.H.; Dahlman, D.L.
Degradation and detoxification of canavanine
by a specialized seed predator. *Science*. 196:
658-660; 1977.
- Rosenthal, G.A.; Dahlman, D.L.; Janzen, D.H.
L-canaline detoxification. A seed predator's
biochemical mechanism. *Science*. 202: 528-529;
1978.
- Scheline, R.R. Mammalian metabolism of plant
xenobiotics. New York: Academic Press; 1978;
502 p.
- Smith, G.S.; Watkins, J.B. Biotransformation of
xenobiotics in tissue of cattle and sheep.
Can. J. Anim. Sci. 64 (Suppl.): 278-280; 1984.
- Sunnerheim, K.; Palo, R.T.; Theander, O.;
Knutsson, P.G. Chemical defense in birch:
platyphylloside, a digestibility reducing
phenol from Betula pendula. Unpublished report.
- Swain, T. Secondary compounds as protective
agents. *Am. Rev. Plant Physiol.* 28: 479-501;
1977.
- Terasawa, M.; Koga, T.; Ouyama, H.; Miyake, M.
Isolation of platyphyllonol, a new diaryl-
heptanoid from green bark of shirakanba,
Betula platyphylla sukatch-var. Japonica hara
J. Japan Wood Res. Soc. 19: 47-48; 1973.
- Terasawa, M.; Koga, T.; Okuyama, H.; Miyake, M.
Phenolic compounds in living tissue of wood
III. *J. Japan Wood Res. Soc.* 30: 391-403; 1984.
- Van Soest, P. The nutritional ecology of the rumi-
nant. Corvallis, OR: O & B Books Inc; 1982;
374 p.
- Zucker, W.V. Tannins: Does structure determine
function? An ecological perspective. *Am. Nat.*
121: 335-365; 1983.

SOUTHERN TEXAS SHRUBS -- NUTRITIVE VALUE AND UTILIZATION BY HERBIVORES

L. W. Varner and L. H. Blankenship

ABSTRACT: Results of three experiments conducted over a 6-year period revealed that southern Texas shrubs were significant components of the diets of white-tailed deer (*Odocoileus virginianus*), jackrabbits (*Lepus californicus*), and beef cattle. Although 13 different shrub species were consumed by all herbivores, major competition among herbivores was for guayacan, cenizo, and mesquite. Diets of the three herbivores were most similar in winter and least similar in spring. Shrubs made up to 35, 97, and 45 percent of the winter diets of jackrabbits, white-tailed deer, and beef cattle, respectively. Among shrub species collected monthly for nutritional analyses, granjeno was the highest in overall quality with annual mean values of 73.3 percent, for *in vitro* digestible dry matter (DDM), 23.8 percent for crude protein (CP), and 0.18 percent for phosphorus (P). Blackbrush was the lowest in DDM of all species, averaging 31.4 percent for the entire year.

INTRODUCTION

Although southern Texas was once a savannah grassland, it is now dominated by a complex mixture of over 25 woody shrubs, trees, and cacti (Johnston 1963). A survey by the Soil Conservation Service in 1963 indicated that 93 percent of southern Texas rangelands were brush-infested, with over 70 percent having dense stands (Smith and Rechenstien 1964). The primary use of southern Texas rangeland is as livestock range; beef cattle are the primary domestic herbivores. In addition, the range provides habitat for white-tailed deer, jackrabbits, cottontail rabbits (*Sylvilagus audubonii*), numerous rodents, and in some areas exotic ruminants.

The shrub component of the southern Texas ecosystem is essential to both domestic and wild herbivores. It provides shade, food, and cover (Inglis 1985). The purpose of this paper is to compare (1) the dietary preferences of major herbivores for indigenous shrubs and (2) the nutritive value of these shrubs.

LOCATION AND METHODS

All three experiments reported were conducted on a 2,040-ha area 45 km southwest of Uvalde, TX,

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that was divided into six pastures, each with a mean size of 340 ha. Dominant soil type, covering 60 percent of the area, was clay loam.

Food habits of jackrabbits, white-tailed deer, and beef cattle were determined on a monthly basis for 14 months from March 1979 to April 1980. Approximately 10 rabbits per month were shot. Their stomach contents were collected and frozen for future diet analyses. In the immediate area where rabbits were shot, five samples each of deer and cattle feces were also collected. Microscope slides of the fecal and stomach material were prepared as described by Hansen and Flinders (1969) and Green and others (1985). Plant species in the sample were determined by the microhistological technique (Sparks and Malechek 1968). Competition for shrubs among the herbivores was evaluated using Kulczynski's similarity index (Oosting 1956). Results for the first year have been summarized and are presented on a seasonal basis. To characterize the nutritive value of an array of southern Texas shrubs, 13 native shrub species were collected monthly from four range sites (sandy loam, clay loam, clay flat, and shallow ridge). Samples from at least 10 plants per site per month were collected for analyses. Samples were separated into leaf, stem, and fruit (when available) components and analyzed for CP (Lauber 1976), DDM (Newman 1972), and P (Kallner 1975). Data from all range sites were averaged.

SHRUB UTILIZATION

Shrub species utilized by the three herbivores are shown in table 1 while scientific names of all species are given in table 2. Only two shrub species were utilized by all three herbivores. Guayacan, one of the few evergreen shrubs in southern Texas, was utilized by all herbivores in winter. Mesquite fruit was used by all herbivores in summer, and mesquite leaves were eaten by jackrabbits during seasons when they were available. Cenizo, guajillo, guayacan, Texas colubrina, and twisted acacia were all used by both deer and cattle.

Similarity in shrub utilization (fig. 1) between jackrabbits and cattle varied from almost 0 percent in spring to over 70 percent in winter. Jackrabbit and deer use of shrubs was most similar in summer and winter because both animals were using large amounts of mesquite fruit and guayacan, respectively. Deer and cattle use of shrubs was most similar in winter (76 percent) because both species used cenizo and guayacan.

Table 1.--Percentage shrubs in diets of southern Texas herbivores

Shrub species	Spring			Summer			Fall			Winter		
	Jack-rabbits	Deer	Cattle	Jack-rabbits	Deer	Cattle	Jack-rabbits	Deer	Cattle	Jack-rabbits	Deer	Cattle
Blackbrush		2.8	>1.0	1.0	10.4	>1.0		24.4			38.5	14.4
Brazil					8.5			5.9			2.9	
Cenizo		1.8				>1.0			9.0		22.8	
Feather dalea				>1.0								
Granjeno					1.3							
Guajillo					2.0	21.1			19.0			
Guayacan	>1.0	33.5	>1.0				>1.0			1.1	18.1	23.1
Lantana								1.8				
Lotebush									>1.0			
Manystem ratany	>1.0									>1.0		>1.0
Mesquite	11.0			19.4	24.9	2.3	11.1			19.9	4.9	5.5
Texas colubrina		9.0	4.7		13.4			10.0				
Twisted acacia		3.1	2.0		16.1			6.7	>1.0			
Vine ephedra			2.5									7.5
Wolfberry										3.0		

Table 2.--Common and scientific names of southern Texas shrub species

Common name	Scientific name
Blackbrush	<i>Acacia rigidula</i>
Brazil	<i>Condalia obovata</i>
Catclaw	<i>Acacia greggii</i>
Cenizo	<i>Leucophyllum frutescens</i>
Coma	<i>Bumelia celastrina</i>
Desert yaupon	<i>Schaefferia cuneifolia</i>
Feather dalea	<i>Dalea formosa</i>
Granjeno	<i>Celtis pallida</i>
Guajillo	<i>Acacia berlandieri</i>
Guayacan	<i>Porlieria angustifolia</i>
Kidneywood	<i>Eysenhardtia texana</i>
Lantana	<i>Lantana microcephala</i>
Lime pricklyash	<i>Zanthoxylum fagara</i>
Lotebush	<i>Condalia obtusifolia</i>
Manystem ratany	<i>Krameria ramossissima</i>
Mesquite	<i>Prosopis glandulosa</i>
Shrubby bluesage	<i>Salvia ballotaeflora</i>
Texas colubrina	<i>Colubrina texensis</i>
Texas persimmon	<i>Diospyros texana</i>
Twisted acacia	<i>Acacia tortuosa</i>
Vine ephedra	<i>Ephedra antisiphilitica</i>
Wolfberry	<i>Lycium berlandieri</i>

Shrub Use By White-tailed Deer

Shrubs were the most consumed forage type for almost all months of the study (fig. 2). Shrub consumption by deer varied from 65 percent of the diet in the spring to over 95 percent in the winter. Since spring forb availability was high, shrub consumption by deer was lowest in March 1979 at 13 percent of the diet (table 3), and was highest during the fall and winter months, averaging over 94 percent from November 1979 through April 1980. The high utilization of shrubs in March 1980 compared to March 1979 was probably caused by lack of forbs in 1980 due to a dry spring. Two shrub species, blackbrush and guajillo, were consumed in significant quantities almost every month of the year. Blackbrush averaged over 12 percent of the diet per month, while guajillo averaged almost 17 percent of the diet each month. Two evergreen species, cenizo and guayacan, were particularly important during the late fall and winter months. Fruit of mesquite and Texas persimmon was particularly important during the summer months.

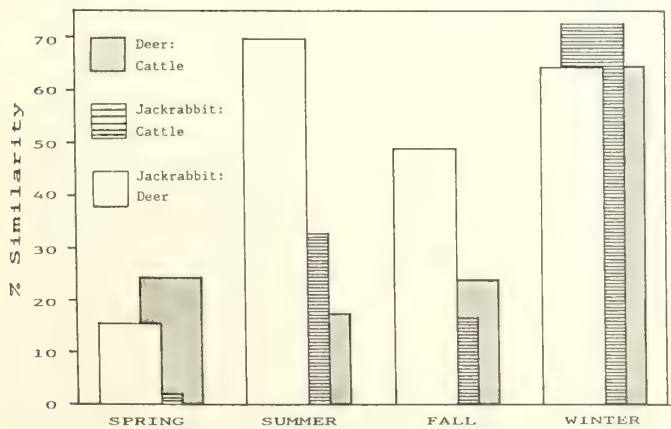


Figure 1.--Percentage similarity in seasonal shrub utilization by southern Texas herbivores.

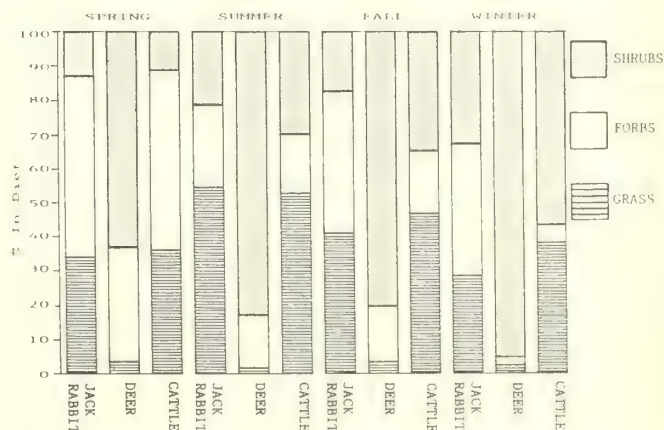


Figure 2.--Seasonal utilization of forage classes by southern Texas herbivores.

Table 3.--Percentage of southern Texas shrubs in white-tailed deer diets over a 14-month period

Shrub species	1979											1980			
	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.		Jan.	Feb.	Mar.	Apr.
Blackbrush	2.4	5.8	29.8	6.9	3.1	14.0		12.9	12.6	19.5		21.6	22.7	17.9	4.1
Cenizo	1.6				4.5				20.9	20.5		12.2	10.0	5.4	23.3
Guajillo	4.0	4.3	11.2	10.8	0.8	14.8	19.5	37.1	35.0	31.6		12.4	13.2	16.6	25.9
Guayacan	3.3	34.5	5.3		17.9			0.7		4.7		6.9	35.9	46.2	23.3
Manystem															
ratany		2.8	4.4	11.0			7.1	5.7		2.1		3.3	1.8	2.2	
Mesquite		0.9		22.3	25.3	21.8	1.1	2.4							
Shrubby															
bluesage	0.3		1.9	1.3		7.1	7.9	12.8				0.3	1.2		4.1
Texas															
persimmon			19.6	6.0	13.0	2.3	0.8		5.4			6.2	3.6	1.3	
Twisted															
acacia		30.6	24.4		4.6	3.5		0.7	5.2	15.6		6.9	5.6	9.2	16.9
Other spp.	1.3	5.1	1.9		10.7	4.3	12.2	8.1	13.3	5.9		6.8	5.6		
Percent shrubs in diet	12.9	84.0	98.5	58.3	79.9	67.8	48.6	80.4	92.4	99.9		76.6	99.6	98.8	97.6

Over the entire study period, four shrub species; guajillo, blackbrush, guayacan, and twisted acacia, consistently made up a significant proportion of deer diets.

Shrub Use By Jackrabbits

Jackrabbits consumed mostly forbs, and grass throughout the year (fig. 2). Of the shrubs consumed, mesquite was the major species eaten during all seasons of the year, varying from 11 percent in spring to 20 percent in winter. Their heaviest utilization of shrubs (35 percent) was during the winter. This agrees with data reported by Westoby (1980) for jackrabbits in Utah.

Shrubs Use By Cattle

Utilization of shrubs by cattle (fig. 2) increased as the year progressed and was 9, 24, 29, and 45 percent of the diet for spring, summer, fall and winter, respectively. Guajillo, and guayacan were the most frequently used shrub species. Three other species, blackbrush, Texas colubrina, and cenizo made up substantial portions of cattle diets during some seasons of the year.

NUTRITIVE VALUE OF SOUTHERN TEXAS SHRUBS

On a seasonal basis DDM of all shrub species was greater in spring and fall than either summer or winter (table 4). Among the shrubs, blackbrush and twisted acacia were the lowest in DDM (< 37.0 percent) during all seasons of the year. Granjeno, the most digestible of all browse species, was never less than 71 percent DDM with an overall mean for the year of 73.3 percent. Guajillo, which was used extensively by both white-tailed deer and cattle, averaged 46.4, 38.9, 41.1, and 35.5 percent DDM during spring, summer, fall, and winter, respectively. Guayacan, which was heavily used

Table 4.--Seasonal in vitro dry matter digestibility of southern Texas shrub species¹

Shrub species	Season				
	Spring	Summer	Fall	Winter	Mean
Blackbrush	34.1 ^f	29.0 ^f	37.0 ^e	25.6 ^f	31.4
Brazil	61.4 ^{cd}	42.3 ^{de}	47.8 ^c	60.4 ^b	53.0
Catclaw	62.2 ^c	36.7 ^e	42.0 ^{de}	47.3 ^d	47.0
Coma	47.9 ^e	47.0 ^d	47.7 ^c	40.3 ^e	45.7
Desert					
yaupon	61.4 ^{cd}	56.0 ^c	58.8 ^b	55.5 ^c	57.9
Granjeno	71.7 ^a	73.3 ^a	75.2 ^a	73.0 ^a	73.3
Guajillo	46.4 ^e	38.9 ^e	41.1 ^e	35.5 ^e	40.5
Guayacan	58.0 ^d	56.6 ^c	60.2 ^b	54.9 ^c	57.4
Kidneywood	62.4 ^c	60.2 ^b	49.8 ^c	54.1 ^c	56.6
Lime					
pricklyash	56.2 ^d	48.1 ^d	73.2 ^a	69.3 ^a	61.7
Lotebush	47.7 ^e	50.7 ^d	38.8 ^e	44.4 ^d	45.4
Twisted					
acacia	32.9 ^f	36.9 ^e	31.9 ^f	28.0 ^f	32.4
Vine					
ephedra	66.4 ^{bc}	54.4 ^c	57.5 ^b	61.2 ^b	60.4
Mean	54.5	48.5	51.0	49.9	51.5

¹Means followed by unlike letters are different (P<0.05).

by jackrabbits, deer and cattle during winter, was 54.9 percent DDM during this time.

Monthly analyses of CP of leaves of major shrub species are shown in figure 3. CP of leaves varied from a low of 11 percent for desert yaupon in January to 40 percent for lotebush in March. Granjeno leaves were among the highest in CP every month of the year, averaging 23.6 percent for the entire year. In southern Texas, because of generally mild winters, even deciduous species such as guajillo, granjeno, and blackbrush keep their leaves longer in the fall, and leaves appear earlier in late winter or spring than forbs or grasses. This accounts for the heavy use of these shrubs and the evergreen shrubs (guayacan and cenizo) by herbivores in winter.

Soils in southern Texas are generally low in P (Fisher 1974). This is reflected in the P content

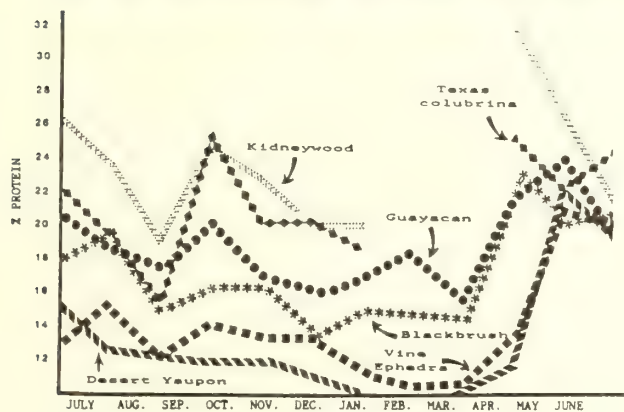
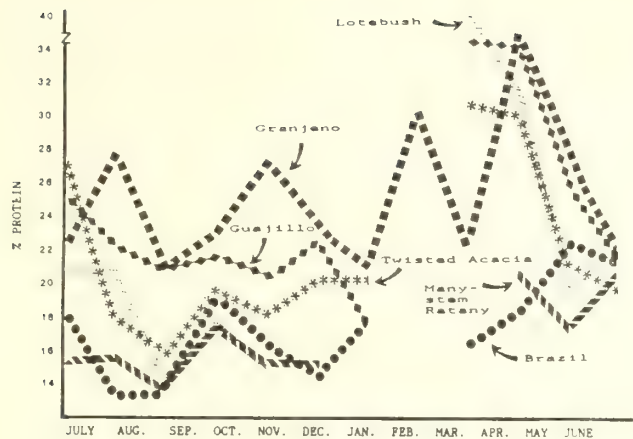


Figure 3.--Monthly protein content of southern Texas shrubs.

of shrub leaves (fig. 4). Over the entire year shrub leaves averaged 0.22 percent P. Guajillo and granjeno were the highest in P of the shrubs, averaging ≥ 0.35 percent in March and April. Guayacan was the lowest in P of shrubs during most months with a mean of 0.14 percent for the entire year.

DISCUSSION

In addition to quality, both quantity and availability of forage during the year are important to herbivores (Wallmo and others 1977). Plants, such as lotebush, that are very high in CP (40 percent) for a short period of time may not greatly improve total nutrient availability to herbivores. In March the twigs of lotebush were approximately 30 percent leaves and 70 percent stems (fig. 5). Stems are less nutritious than leaves (Sullivan 1969). Therefore, not only the quality of a particular forage species, but the quantity of leaves in relation to stems should be considered when determining which species to manage for to improve the nutrient intake of rangeland herbivores.

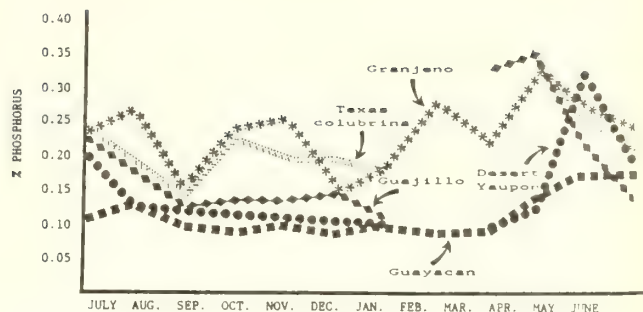


Figure 4.--Monthly phosphorus content of southern Texas shrubs.

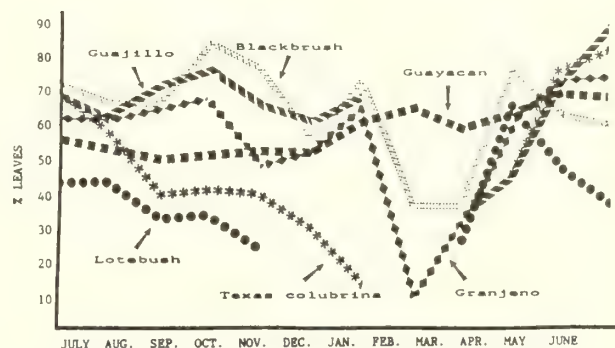


Figure 5.--Leaves as a percent of dry matter of southern Texas shrubs.

Knowledge of herbivore food habits must be correlated to knowledge of the nutritional quality of species consumed before we can coordinate deer and livestock management with vegetation changes. Plants that do not appear, in laboratory analyses, to be extremely high in nutritive value (such as blackbrush or twisted acacia) still may be important sources of nutrient to herbivores. They may, for reasons that are not apparent from routine laboratory analyses, be highly palatable to a particular herbivore. We need a better understanding of why some species are selected at certain times of the year and not at others and why some species that appear to be good sources of nutrients are rarely selected.

These data demonstrate that a diversity of plant species in the habitat allows herbivores to select a diet that is both nutritious and palatable. In addition, both numbers and kinds of herbivores may have to be manipulated to reduce competition for available high-quality forage species.

REFERENCES

- Fisher, F.L. Native nutrient status of Texas soils. Misc. Publ. L-1054. College Station, TX: Texas Agricultural Extension Service. 1974 6 p.
- Green, B.L., Blankenship, L.H.; Cogar, V.F.; McMahon, T. Wildlife food plants -- a microscopic view. Kleberg Studies in Natural Resources. College Station, TX: Texas A&M University. 1985 100p.
- Hansen, R.M.; Flinders, J.F. Food habits of North American hares. Range Science Department, Science Series No. 1. Fort Collins, CO: Colorado State University; 1969. 18 p.
- Inglis, J.M. Wildlife management and IBMS. Publ. B-1493. College Station, TX: Texas Agricultural Experiment Station; 1985. 71 p.
- Johnston, M.C. Past and present grasslands of southern Texas and northeastern Mexico. Ecology. 44: 456-466; 1963.
- Kallner, A. Determination of phosphate in serum and urine by a single step malachite green method. Clinica Chem. Acta. 59: 35-39; 1975.
- Lauber, K. Photometric determination of nitrogen: wet incineration followed by formulation of indophenol blue with salicylate/hypochlorite. Clinica Chem. Acta. 67: 107-110; 1976.
- Newman, D.M.R. A modified procedure for large scale pasture evaluation by digestibility in vitro. Austral. J. Agric. Sci. 46: 212-213; 1972.
- Oosting, H.J. The study of plant communities. San Francisco, CA: W.H. Freeman and Co.; 1956. 400 p.
- Smith, H.N.; Rechenstien, C.A. Grassland restoration -- the Texas brush problem. Unnumbered publ. U.S. Department of Agriculture, Soil Conservation Service; 1964. 17 p.
- Sparks, D.R.; Malechek, J.C. Estimating percentage dry weights in diets using a microscope technique. J. Range Manage. 21: 264-265; 1968.
- Sullivan, J.T. Chemical composition of range forages with reference to the needs of the grazing animal--a review of recent research findings. Publ. 34-107.: U.S. Department of Agriculture, Agricultural Research Service; 1969. 113 p.
- Wallmo, O.C., Carpenter, L.H.; Regelin, W.L.; Gill, R.B.; Baker, D.L. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30: 122-128; 1977.
- Westoby, M. Black-tailed jackrabbit diets in Curlew Valley, northern Utah. J. Wildl. Manage. 44: 942-948; 1980.

THE RELATIONSHIP OF TETRADYMIA SPECIES AND ARTEMISIA NOVA

TO PHOTSENSITIZATION IN SHEEP

A. Earl Johnson

ABSTRACT: Photosensitization of sheep caused by toxins in Tetradymia canescens and T. glabrata is widespread in the Great Basin. The toxins damage animal livers in such a way that phylloerythrin, a photosensitizing byproduct of chlorophyll-rich food, is not removed from the bloodstream before it reaches the peripheral circulation. Although utilization of Tetradymia as a food is limited, during stressful situations it may be heavily eaten. Rapid liver and epidermal damage may cause death or abortion. Efforts to produce secondary photosensitization experimentally in sheep were frustrated until it was discovered that ingestion of Artemisia nova produced greater sensitivity to Tetradymia phototoxins. Possible mechanisms of interaction between the two plant species are explored.

INTRODUCTION

Tetradymia spp. are spinescent or glabrous, generally canescent shrubs that begin growth early in the spring and bloom in spring or summer. They are found scattered throughout the Great Basin and extend into southern California and British Columbia. There are 10 to 20 species of Tetradymia depending on the method of classification. Of the two species of concern here, T. canescens (spineless horsebrush) (fig. 1) is the more far-ranging and may be found throughout the Great Basin. Tetradymia glabrata (littleleaf horsebrush or coal oil brush) (fig. 2) is also widespread but occurs in greater numbers in the more central portions of the Great Basin. Both species are utilized as food by sheep but generally are grazed sparingly, with young shoots and buds having the greatest palatability. Tetradymia glabrata often becomes green well before other more palatable plants and is more heavily utilized at these times and during stormy periods when sheep may alter their grazing habits.

Fleming (1922) in Nevada alerted the livestock industry to the fact that T. glabrata (then called spring rabbitbrush) was poisonous to sheep but not harmful to cattle. He determined, through

experimental feeding, that sheep could be seriously damaged or killed with relatively small daily doses of the plant within a 3- to 4-day period. Sheep fed larger doses became sick almost immediately and died within 24 hours. He noted that the liver was severely affected as evidenced by discoloration and friability grossly, and by hepatic necrosis, fibrosis, and fatty degeneration microscopically.



Figure 1.--Tetradymia canescens (spineless or little grey horsebrush) is often found in the more semiarid regions of the Great Basin. It has a distinctly grey color compared to sagebrush and other plants that usually accompany it. Its leaves are larger and softer than those of T. glabrata and their odor is not as distinct.

Fleming did not mention photosensitization and it was not until 15 years later that Clawson and Huffman (1937) incriminated, through field observation and experimental feedings, both T. glabrata and T. canescens as causative agents in "bighead," a photosensitization syndrome in sheep characterized mainly by swelling of the sheep's head.

PHOTSENSITIZATION

Photosensitization Versus Sunburn

Photosensitization is sometimes referred to as "sunburn," but there is a distinct difference between sunburn and photosensitization. Sunburn is caused by undue exposure to ultraviolet radiation of light wavelengths shorter than 320

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A



B

Figure 2.--*Tetradymia glabrata* (littleleaf horsebrush or coal oil brush) is a woody plant usually 1 to 2 feet tall (A) that grows in the more arid parts of the Great Basin. It is named for its small, dark-green leaves (B) that emit a pungent coal oil-like odor.

nanometers (nm) and results from the direct action of these ultraviolet rays on epidermal cells (Daynes and Spikes 1983). It is a normal reaction in unprotected, unpigmented skin, and the reaction is usually delayed for several hours after exposure to light. On the other hand, photosensitization involves a reaction to light of a specific photosensitizing compound that has been eaten by livestock and found its way to the skin through peripheral blood circulation. The photosensitizing compound may be found in plants or in food contaminants. In the skin it absorbs large amounts of damaging ultraviolet rays of specific wavelengths from the sun, and becomes activated or converted into a highly excited state. In this excited state, molecules of the photosensitizing agent transfer damaging energy to adjacent cellular components, disrupting a variety of cellular activities. Without light the agent is nontoxic, but on exposure to light the reaction is immediate and usually more devastating than sunburn.

Photosensitization Types

Plant photosensitizing reactions are of two types, primary and secondary. In primary photosensitization the sensitizing compound is in a plant, and as the plant is eaten the compound is absorbed and reaches the skin unchanged (Clare 1955). St. John's wort (*Hypericum perforatum*) and spring parsley (*Cymopterus watsonii*) are examples of plants containing primary photosensitizers. In secondary photosensitization, phylloerythrin is the photosensitizing agent (Clare 1955). Phylloerythrin is a byproduct of chlorophyll and is formed in the digestive tract of any ruminant eating green feed. In a normal animal, phylloerythrin is removed from the blood by the liver and secreted in the bile before it can reach the peripheral circulation. Any plant toxin or other agent that damages the liver in such a way that it loses its ability to remove the phylloerythrin may

then cause secondary or hepatogenous photosensitization. Thus, there are two requirements for secondary photosensitization to occur: the animal must be eating chlorophyll-rich food, and the liver of the animal must be damaged in such a way that it cannot remove and secrete phylloerythrin formed from the chlorophyll. Most livestock photosensitizations are of this secondary type.

Photosensitization Effects in Sheep

Liver damage caused by *Tetradymia* and the accompanying photosensitization is often a devastating occurrence. When sheep have grazed sufficient *Tetradymia*, the problem can develop rapidly with several hundred sheep becoming affected in a 2- to 3- hour period. In the early stages of photosensitization the sheep become uncomfortable and seek places to rub or scratch their heads. Restlessness, swollen lips, and heavy drooping ears are usually the first signs noted by the herder, and some sheep may assume an uncharacteristic stance with the head elevated and nose pointed upward. They lose their herding instinct, begin to seek shade, and may scatter over an area of several square miles. Facial tissues may swell to the extent that they crack, with serum exudation and heavy scab formation. Secondary infection may occur if treatment is not initiated. Scabbing may cause impaired vision in some sheep. In some primary photosensitizations scarring of the eye may occur with total blindness as a result. Wool in some sheep may sluff, and repair of these areas may not occur. Sheep that have consumed larger *Tetradymia* doses may become sick from liver injury and may abort fetuses that are usually in the last trimester of development. The only means of treating affected sheep is to provide good food and shade and treat the symptoms. This usually requires transporting sheep to the home ranch which may be many miles away. Sheep thus treated may survive depending on the degree of liver damage and photosensitization.

The loss of a ewe also involves the loss of the full fleece that she is carrying and the loss of her fetal lamb. If she survives, she is often a nonproductive animal.

EXPERIMENTAL AND FIELD OBSERVATIONS

Even though the textbook explanation of secondary photosensitization seems rather straightforward and simple, our early attempts to experimentally produce this photosensitization quickly revealed that it was not simple. We experienced failure after failure (Johnson 1974a). A review of the literature, meager though it was, gave no clues; neither did frequent consultations with livestock owners who had had the problem. Observation of grazing habits of sheep on Tetradymia-infested ranges also gave no clues. We learned, however, that the problem did not occur annually, but usually only when certain environmental and management conditions meshed. Furthermore, sheep owners that had the problem in 2 or more successive years were alert and careful to manage their sheep to avoid Tetradymia, but sheep owners whose herds escaped the problem for a year or two became complacent and their herds were highly susceptible to the problem.

A greater appreciation of the severity of the problem was gained as more affected herds were observed. Tetradymia-infested areas where many outbreaks occurred were often 100 to 200 miles from the home ranch, so the herder or sheep owner had to deal with the problem as best they could with little or no means. We noted that isolated cases of Tetradymia-related photosensitization commonly occurred on Tetradymia-infested ranges, but sheep utilized very little Tetradymia as food in most situations. Many of the toxicity and photosensitization problems occurred along old trails and driveways. Here the Tetradymia grows in greatest abundance and the sheep are often exposed to more stressful situations than would normally be encountered when free ranging. Often these trailing sheep may be pushed along at a faster than desirable rate to maintain an allotted time schedule; they may be held up in undesirable areas while waiting for another herd to move on; they may be unduly hungry when they reach a water hole; and after drinking they may wish to eat immediately. Often Tetradymia is plentiful with little other feed available near these watering areas. Sheep, as do other animals, sometimes seem able to detect an impending storm and may change their grazing habits to "stock up" on food before the storm arrives; more Tetradymia than normal may be eaten under these conditions. Spring snows sometimes briefly cover low-growing food plants so that the taller growing Tetradymia is more available and thus may be grazed more heavily than desirable. In some years, moisture and temperature conditions allow palatable forage to grow as early as the Tetradymia so that Tetradymia is not a hazard.

As these observations were made, our efforts to produce photosensitization experimentally with the plant continued. We were convinced that it was

just a matter of giving the right plant dosage in the right time period. But after feeding every reasonable dose at a multitude of time intervals and causing only occasional photosensitization, it became apparent that other factors must account for the failures. Liver damage and even death could be produced with relatively small Tetradymia dosages fed in a 36- to 48-hour period, but the occasional resultant photosensitization seemed to happen randomly and could not be correlated with dosage.

In seeking causes for our failure we conducted experiments to determine if the responsible toxin had volatilized or was enzymatically degraded in the time lapse between collecting the Tetradymia and feeding it (Johnson 1974a). To minimize this time interval and to assure that light conditions were similar at the laboratory and on the range areas where outbreaks occurred, sheep were transported to field areas and fed Tetradymia there. Results remained negative.

At about this stage of the investigation, reasons for Clawson's and Huffman's (1937) success and our failure became a great concern. While delving into some of Clawson's unpublished records, we noted that they also had difficulty in some experiments and that the successful experiments were on sheep taken immediately from range herds. Therefore, sheep from the laboratory were taken to the problem range area, and other sheep were obtained from herds grazing the range. Both groups were fed Tetradymia. Sheep from the laboratory were non-reactive; those from the range area were photosensitized. It seemed that progress was finally being made, but confirmation of results was needed. A repeat trial the following year produced essentially negative results, so again confusion reigned.

Further evaluation of Clawson's and Huffman's unpublished records revealed that they had also noted the correlation between the range sheep and their susceptibility to Tetradymia and had attempted to precondition their laboratory sheep by first experimentally feeding bud sage (Artemisia spinescens), black sagebrush (Artemisia nova), big sagebrush (Artemisia tridentata), hopsage (Grayia spinosa), winterfat (Eurotia lanata), shadscale (Atriplex confertifolia), and greasewood (Sarcobatus vermiculatus), and combinations of these (Johnson 1974b). They obtained some success with black sagebrush and big sagebrush. Armed with this information, we returned to the problem range to determine why we had been successful one year and failed the next. The answer came with the discovery that the sheep in our first successful experiment had been grazing range that was made up mostly of black sagebrush (fig. 3). Sheep used the following year in the unsuccessful attempt were taken from a location where there was little or no black sagebrush.

Subsequent experiments in which black sagebrush was fed prior to feeding Tetradymia have been much more successful in producing photosensitization, although it cannot be produced with complete regularity.



A



B

Figure 3.--*Artemisia nova* (black sagebrush) is a low-growing, dark-colored sagebrush of the tridentata type (A). It grows on well-drained gravelly or rocky slopes and is a palatable and nutritious winter food for sheep (B).

These experiments have also indicated that black sagebrush alone can be lethal to sheep when large amounts are fed without allowing the sheep to gradually adapt to the plant, and that small non-toxic doses of *Tetradymia* fed to sheep can be made toxic if black sagebrush is fed in small amounts for a few days previously.

Black sagebrush is good feed for sheep on many winter ranges in Utah and Nevada. It has a high protein content, and sheep on many of these ranges could not survive without it. However, it obviously contains toxic compounds, and at times, may be the unrecognized source of sheep problems. Some sheep owners have reported that they believe lush black sagebrush eaten by their sheep in early spring to be the source of abortion problems.

There is little doubt that there is a synergistic toxic relationship between black sagebrush and *Tetradymia glabrata* and *T. canescens*. We have conducted several experiments confirming this. *Tetradymia glabrata* is more toxic than *T. canescens*, and better success in causing photosensitization is usually obtained with *T. canescens*, probably because of its lesser toxicity. It does not kill the animal before photosensitization can occur, as *T. glabrata* often does. The precise nature of the toxic relationship of these two plants is not apparent at this time because the mechanism of absorption of phylloerythrin by liver cells and the method of its excretion into the biliary system are not known. Furthermore, the chemical nature of the toxin, in either *Tetradymia* or black sagebrush, responsible for the liver damage is not known. One of the compounds in *T. glabrata* toxic to mice has been identified, but its toxicity has not been confirmed in sheep (Jennings and others 1974). The sagebrushes contain several chemical classes of compounds, such as simple terpenes (essential oils) and sesquiterpene lactones, that could be responsible. Terpenes have been shown to alter the rumen microflora in deer (Nagy and others

1964), which might affect their ability to utilize certain feed types. If terpenes have this effect in sheep, the ability of the sheep's digestive tract to either detoxify or utilize the *Tetradymia* toxin may be altered, thus altering its toxicity.

Another possible mechanism in the relationship of these two plants may be that sagebrush induces or depletes liver microsomal enzymes that may be functional in the toxicity of *Tetradymia*.

Sagebrush toxins may injure the liver cell membrane, altering the cell's ability to absorb phylloerythrin or blocking its excretion into the biliary system. At present the histological effects on the sheep's liver of black sagebrush fed alone are being compared with the effects of *T. glabrata* fed alone and with the effects of the two plants fed in combination. Thus far, it appears that changes may be too subtle to be detected by light microscopy and may require scrutiny at the sub-cellular level by electron microscopy. The lesion may be purely biochemical and require biochemical or histochemical means of detection.

The relationship of these two plants is extremely interesting and raises questions concerning the possible ancillary relationships of other common range plants to toxicities in livestock by known poisonous plants.

REFERENCES

- Clare, N. T. Photosensitization in animals. *Advances in Veterinary Science*. 2: 182-211; 1955.
- Clawson, A. B.; Huffman, W. T. Bighead in sheep caused by plant poisoning. *National Woolgrower*. 27: 13-16; 1937.

- Daynes, Raymond A.; Spikes, John D., eds. Experimental and clinical photoimmunology. Vol. 1. Boca Raton, FL: CRC Press; 1983. 210 p.
- Fleming, C. E.; Miller, M. R.; Vawter, L. R. The spring rabbit-brush, a range plant poisonous to sheep. Bulletin 104. Reno, NV: University of Nevada, Agricultural Research Station; 1922: 1-29.
- Johnson, A. Earl. Experimental photosensitization and toxicity in sheep produced by Tetradymia glabrata. Canadian Journal of Comparative Medicine. 38(4): 406-410; 1974a.
- Johnson, A. Earl. Predisposing influence of range plants on Tetradymia related photosensitization in sheep. American Journal of Veterinary Research. 35(12): 1583-1585; 1974b.
- Jennings, Paul W.; Reeder, Samuel K.; Hurley, Jerome C.; Caughlan, Charles N.; Smith, David G. Isolation and structure determinations of one of the toxic constituents from Tetradymia glabrata. Journal of Organic Chemistry. 39: 3392-3398; 1974.
- Nagy, Julius G.; Steinhoff, Harold W.; Ward, Gerald M. Effects of essential oils of sagebrush on deer rumen microbial function. Journal of Wildlife Management. 28(4): 785-790; 1964.

PRENATAL AND NEONATAL DEATH OF LAMBS DUE TO MATERNAL

GRAZING OF VERATRUM CALIFORNICUM

Richard F. Keeler

ABSTRACT: Veratrum californicum (false hellebore), when ingested by pregnant ewes, causes prenatal and neonatal lamb mortality. Secondary compounds from the plant such as cyclopamine, jervine, and cycloposine are possibly responsible. These steroidal alkaloids exert teratogenic and embryotoxic effects. "Monkey face lamb" disease involving craniofacial defects, commonly fatal, is induced by ingestion of the plant on day 14 of gestation. Ingestion on days 19, 20, or 21 induces early embryonic deaths. Severe congenital tracheal stenosis, resulting in death of lambs immediately after parturition, along with shortening of various fore and rear limb bones are induced by daily ingestion over 2- or 3-day periods during days 27 through 33 of gestation. Collective mortality from these conditions might reduce the viable lamb crop by half. Allowing pregnant ewes to graze V. californicum before the 33d day of gestation cannot be recommended, and may be a significant factor in lamb crop losses that have been otherwise unexplained.

INTRODUCTION AND BACKGROUND STUDIES

The birth defects induced in lambs by maternal ingestion of the plant Veratrum californicum (false hellebore) (fig. 1) during gestation have been studied for several years. Cyclopia and related craniofacial deformities, called "monkey face lamb" disease by ranchers, are induced in lambs when ewes consume the plant on day 14 of gestation (Binns and others 1962, 1963, 1964, 1965). Deformities have occurred in up to 25 percent of the lambs from some range sheep flocks (Binns and others 1963, 1964). The classic expression of the disease (Binns and others 1961) is a true cyclopia (fig. 2) usually with a proboscis above the eye and severely shortened maxilla and premaxilla bones. There may be severe brain involvement with only a rind of cerebral tissue evident in some cases. Cyclopics have only one optic nerve, and the skull is altered accordingly. Lambs with mild defects show only a shortening of the maxilla and premaxilla. Severe cases die. Some mild cases may survive.

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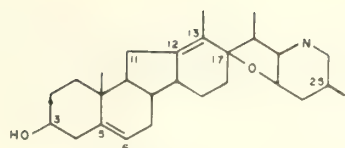


Figure 1.--The range plant Veratrum californicum.

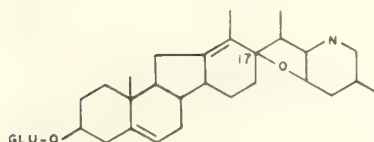


Figure 2.--"Monkey face lamb" disease induced by maternal ingestion during gestation of Veratrum californicum.

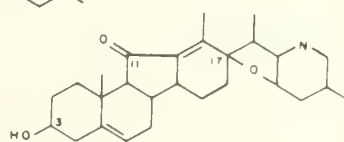
Susceptibility to deformity is restricted to day 14 of gestation (assigning the day after breeding as day zero of gestation)(Binns and others 1965). This sharply limited period led to recommendations that pregnant sheep be denied access to the plant until 14 days after removal of rams, a practice relatively easy to follow. Ranchers commonly pursue this practice, and this has resulted in a dramatic reduction in incidence of "monkey face lamb" disease.



CYCLOPAMINE



CYCLOPOSINE



JERVINE

Figure 3.--Cyclopia-inducing steroidal alkaloids of Veratrum californicum.

Certain secondary plant alkaloids proved to be responsible for the observed effects. Through extraction and isolation of alkaloids from the plant coupled with administration of the fractions and alkaloids to pregnant sheep on day 14 of gestation, it was possible to identify three alkaloids from among several dozen in the plant that could induce the condition (Keeler and Binns 1966a, 1966b; Keeler 1970, 1984). Those three alkaloids are cyclopamine, cycloposine, and jervine (fig. 3). All three are C-nor-D-homo steroidal alkaloids of the jeveratrum series with a furanopiperidine function spiro at carbon 17 of the steroid. All are closely similar--cyclopamine being 11-deoxojervine and cycloposine the 3-glucosyl glycoside of 11-deoxojervine. Both structure and configuration play essential roles in the teratogenic potency; the ether bridge is particularly critical (Keeler 1984) because of its influence on the configurational position of the essential nitrogen atom. Experiments in laboratory animals with Veratrum alkaloids, analogs, and various related model compounds suggested that the nitrogen atom had to be in an α -configurational position (fig. 4) with respect to the steroid portion of the molecule for the compound to be teratogenic (Keeler 1984).

Ranchers whose sheep flocks graze areas with abundant V. californicum, and who have experienced a high incidence of "monkey face lamb" disease, have also complained on occasion of "low lamb crops" (Binns and others 1963; Van Kampen and others 1969). Furthermore, laboratory observations of experimental sheep fed V. californicum indicated possible prenatal loss. Van Kampen and others (1969) collected and summarized data from previous experiments at our laboratory on the outcome of pregnancy in ewes gavaged (fed by stomach tube) the aerial portion of V. californicum at various gestational periods up to the 30th day. Pregnant ewes (361 from multiple breedings) had been gavaged. None cycled at regular intervals since they were multiple-bred (bred on 3 or 4 successive days) to achieve as

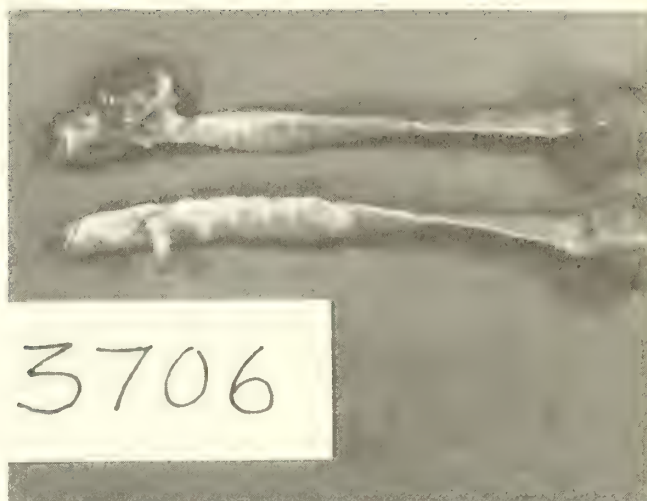


Figure 4.--Congenital tracheal stenosis in twin lambs induced by maternal ingestion of Veratrum californicum during gestation.

near 100 percent conception as possible. But 60 (17 percent) came back into estrus later at irregular intervals, suggesting that embryonic death had occurred. Nineteen (5 percent) aborted, 43 (12 percent) had "monkey face" lambs, and 239 (66 percent) had normal lambs. There was a total prenatal and neonatal loss of 34 percent from embryonic death, abortion, or deformity. Among 66 single-bred controls, eight (12 percent) rebred at regular cycle intervals indicating failure to conceive to the single breeding. The other 58 controls delivered normal lambs. These observations suggested that considerable lamb loss may occur from V. californicum ingestion. The observations were consistent with the complaints by sheep ranchers of low lamb crops from ewes that had grazed areas with abundant V. californicum during gestation.

RECENT STUDIES AT THE POISONOUS PLANT LABORATORY

In recent experimental studies at our laboratory on the hazards of Veratrum ingestion in sheep, we have used groups of Columbia/Rambouillet cross ewes, single bred to Columbia rams with the day of breeding considered day zero of gestation. These ewes were then gavaged 30-50 g per ewe per dose of the root/rhizome portion of dried, ground V. californicum in water slurry at selected days of gestation. Plant material was collected in Muldoon Canyon, ID. The root/rhizome rather than aerial portion of the plant was used because concentration of the teratogenic alkaloids is about 10 times as high in the root/rhizome (Keeler and Binns 1971). Since a great deal was already known about hazards of ingestion of the plant on or about day 14 (Binns and others 1963, 1965), we conducted a preliminary study in 1980 to determine if there were hazards to the conceptus from maternal ingestion of the plant between days 19 and 42 of gestation. In groups of ewes gavaged plant material daily over 3-day periods, results suggested a prenatal death hazard related to administration on days 19 through 21, and a

neonatal death hazard related to administration on days 28 through 30 or 31 through 33. In the day 28 through 30 and day 31 to 33 groups, some lambs that died shortly after birth also had limb deformities of the type previously found to occur at about that gestation period (fig. 5)(Binns and others 1972). No harmful effects were observed between days 33 and 42, and from an embryologic point of view, problems would be unlikely beyond day 42. Experiments designed to test more rigorously the mortality of concepti resulting from gavage of plant material during days 19 through 21 and 28 through 33 were clearly needed. Such experiments were performed during the next 5 years.

In one of those experiments, nine ewes were administered plant material on days 19, 20, and 21 of gestation. Two ewes lambed (22 percent), and seven (78 percent) failed to lamb. Among controls only two of nine (23 percent) failed to lamb, likely because they failed to conceive after the single breeding. Using as comparison the two of nine controls that failed to lamb, we can calculate the number and percentage of treatment ewes that probably terminated their pregnancies by early embryonic death from V. californicum ingestion as: 9 minus 2 that lambed minus 2 expected not to conceive = 5 [5 of 9 (56 percent) $P < 0.0005$]. Ingestion of the plant on days 19, 20, and 21 resulted in a high incidence of early embryonic death.

In another experiment, six pregnant ewes were administered Veratrum on days 31, 32, and 33 of gestation and six on days 28, 29, and 30. Ten of 19 lambs in these two groups died within minutes after birth. Six of the 10 that were autopsied had tracheal stenosis that prevented respiration and caused death. Only one of 12 lambs born to seven control ewes died directly after birth. It did not have tracheal stenosis. The tracheal stenosis induced by Veratrum was characterized by lateral flattening throughout the entire length of the trachea due to hypoplastic and disoriented tracheal rings. The nonpatent rings resulted in a nondistended lumen (fig. 4) through which no air could pass when the newborn lambs attempted to breathe (Keeler and others 1985). Ten of the 19 lambs born to treatment ewes also had limb defects that we had previously found to be induced at this period by either plant material or a cyclopamine preparation (Binns and others 1972; Keeler 1973), while none of the controls were so affected. Those limb defects were generally characterized by a shortening of both of the metacarpal or both of the metatarsal bones, or a shortening of all four bones (fig. 5).

A similar experiment was conducted to confirm that tracheal stenosis was induced by the plant. Plant material was gavaged to groups of pregnant ewes for 2- or 3-day intervals between the 28th and 32d days of gestation. All 12 ewes in these groups were killed 3 days prior to parturition for autopsy of fetuses. Sixteen of 24 lambs (67 percent) had tracheal stenosis and 23 of 24 (96 percent) had limb defects confirmed by autopsy of defleshed specimens. The limb defects in six of



Figure 5.--Congenital short metacarpal and metatarsal bones in a lamb induced by maternal ingestion of Veratrum californicum during gestation.

these lambs were not apparent except through careful measurements of bone lengths at autopsy and after drying of the defleshed specimens. Perhaps half of the 23 lambs with limb defects would not have been considered defective under field conditions, because limbs were only slightly shortened. Five control lambs from four control ewes had no tracheal stenosis nor limb defects.

Additional experiments were conducted in 1985 that confirm all of these observations. Summarizing all experiments to date, 13 of 16 ewes (81 percent) dosed with V. californicum on days 19 through 21 of gestation failed to deliver lambs. Only two of 13 control ewes (15 percent) failed to lamb; this clearly demonstrates the ready induction of embryonic death by Veratrum ingestion. Furthermore, to date, 31 of 76 lambs (41 percent) born to 46 ewes gavaged the plant for 2- or 3-day intervals between days 27 and 33 of gestation had tracheal stenosis; none of the 32 lambs born to 21 control ewes had the condition. This clearly demonstrates the propensity of the plant to induce this defect, which is lethal within moments after birth.

Whether any or all of the three known teratogenic alkaloids are responsible for the tracheal stenosis and early embryonic death remains to be seen. They do induce "monkey face lamb" disease (Keeler 1970, 1984). Cyclopamine was tested for induction of shortened limbs and found active (Keeler 1973), although further tests were inconclusive. Preliminary experiments suggest cyclopamine may induce tracheal stenosis, although no severe cases have yet been induced. No trials have been completed with cyclopamine on days 19 through 21 to test its propensity to induce early embryonic death. But both cyclopamine and jervine induced excessive resorptions (embryonic and fetal deaths) in hamsters (Keeler 1975).

RISKS AND RECOMMENDATIONS

Table 1 summarizes lamb crop losses under experimental conditions from maternal ingestion of Veratrum californicum at various gestation periods, and compares them to actual or potential lamb crop losses under field conditions. Taken into consideration are losses due to "monkey face lamb" disease induced by day 14 ingestion, early embryonic deaths induced by day 19 to 21 ingestion, and neonatal deaths due to tracheal stenosis induced by day 27 to 33 ingestion. Expected incidence in the field is difficult to judge, but we estimate the field incidence of early embryonic death and tracheal stenosis would not exceed one quarter of the laboratory incidence because the highest experimental incidence (Binns and others 1965) of cephalic defects was 100 percent compared to the highest reported field incidence of 25 percent (Binns and others 1963). Consequently, potential field incidence of tracheal stenosis might reach 10 percent, and that of early embryonic death might reach 20 percent. But the figures of 25 percent, 10 percent, and 20 percent for each of the three conditions might represent a collective lamb crop loss of nearly 50 percent.

Totaling from the tables the "days at risk" (days 14, 19-20-21, 27-28-29-30-31-32-33) for the conceptus, resulting from maternal grazing of V. californicum, we have several days of potential hazard with some much more hazardous than others.

Table 1.--Lamb crop loss induced by Veratrum californicum ingestion by pregnant ewes under experimental laboratory conditions compared to actual or potential loss under field conditions

	Death from cyclopia and related defects (14th day ingestion)	Apparent embryonic deaths (19-21 day ingestion)	Deaths from trachael stenosis
	-----Percent-----		
Laboratory conditions	Up to 100	¹ 81	¹ 41
Field conditions	Up to 25 (actual)	² About 20 (potential)	² About 10 (potential)

¹Collective incidence in all experiments through 1985.

²Potential loss based on the assumption that field cases might equal 25 percent of experimental laboratory cases as in column one.

What then is a prudent grazing policy for pregnant sheep in areas with an abundance of Veratrum californicum? During the 20-day period from day 14 to day 33 the conceptus is at risk from maternal grazing of the plant about half the time with a potential lamb crop loss of near 50 percent. The value of lambs lost plus attendant losses can easily exceed the value of forage consumed during the first 33 days of gestation. Consequently, a prudent recommendation must be that ranchers not allow pregnant sheep access to Veratrum californicum until all ewes have passed the 33d day of gestation.

REFERENCES

- Binns, W.; Anderson, W. A.; Sullivan, D. J. Further observations on a congenital cyclopian-type malformation. J. Am. Vet. Med. Assoc. 137: 515-521; 1961.
- Binns, W.; James, L. F.; Shupe, J. L. Congenital malformations in lambs reproduced by feeding a poisonous range plant. The Southwestern Veterinarian. 17: 221-223; 1964.
- Binns, W.; James, L. F.; Shupe, J. L.; Everett, G. A congenital cyclopian-type malformation in lambs induced by maternal ingestion of a range plant, Veratrum californicum. Am. J. Vet. Res. 24: 1164-1175; 1963.
- Binns, W.; James, L. F.; Shupe, J. L.; Thacker, E. J. Cyclopian-type malformation in lambs. Arch. Environ. Health. 5: 106-108; 1962.
- Binns, W.; Keeler, R. F.; Balls, L. D. Congenital deformities in lambs, calves, and goats resulting from maternal ingestion of Veratrum californicum: harelip, cleft palate, ataxia, and hypoplasia of metacarpal and metatarsal bones. Clin. Toxicol. 5: 265-261; 1972.
- Binns, W.; Shupe, J. L.; Keeler, R. F.; James, L. F. Chronologic evaluation of teratogenicity in sheep fed Veratrum californicum. J. Am. Vet. Med. Assoc. 147: 839-842; 1965.
- Keeler, R. F. Teratogenic compounds of Veratrum californicum (Durand). IX. Structure activity relation. Teratology. 3: 169-173; 1970.
- Keeler, R. F. Teratogenic compounds of Veratrum californicum (Durand). XIV. Limb deformities produced by cyclopamine. Proc. Soc. Exp. Biol. Med. 142: 1287-1291; 1973.
- Keeler, R. F. Teratogenic effects of cyclopamine and jervine in rats, mice and hamsters. Proc. Soc. Expt. Biol. Med. 149: 302-306; 1975.
- Keeler, R. F. Mammalian teratogenicity of steroidal alkaloids. In: Ness, W. D.; Fuller, G.; Tsai, L-S., eds. Biochemistry and function of isopentenoids in plants. NY: Dekker, Inc. 1984: 531-562.

- Keeler, R. F.; Binns, W. Teratogenic compounds of Veratrum californicum (Durand). I. Preparation and characterization of fractions and alkaloids for biologic testing. Can. J. Biochem. 44: 819-828; 1966a.
- Keeler, R. F.; Binns, W. Teratogenic compounds of Veratrum californicum. II. Production of ovine fetal cyclopia by fractions and alkaloid preparations. Can. Jour. Biochem. 44: 829-838; 1966b.
- Keeler, R. F.; Binns, W. Teratogenic compounds of Veratrum californicum as a function of plant part, stage, and site of growth. Phytochemistry. 10: 1765-1769; 1971.
- Keeler, R. F.; Young, S.; Smart, R. Congenital tracheal stenosis in lambs induced by maternal ingestion of Veratrum californicum. Teratology. 31: 83-88; 1985.
- Van Kampen, K. R.; Binns, W.; James, L. F.; Balls, L. D. Early embryonic death in ewes given Veratrum californicum. Am. J. Vet. Res. 30: 517-519; 1969.

PRIMARY PHOTOSENSITIZATION IN LIVESTOCK BY RANGE PLANTS

M. Coburn Williams

ABSTRACT: Primary photosensitization is caused by skin contact or ingestion of phototoxic compounds that occur in the plant families Apiaceae, Rutaceae, Moraceae, Fabaceae, Hypericaceae, and Polygonaceae. The phototoxicity of spring parsley (*Cymopterus watsonii*) in ewes causes udder inflammation and sensitivity and results in significant losses of lambs from starvation and dehydration in southwestern Utah. This plant can be controlled with 2,4-D ester or 2,4-D amine applied at 2 lb/acre.

INTRODUCTION

Species of several plant genera produce photodynamic compounds that cause primary photosensitization in animals and birds (Pathak and others 1962). The photodynamic compound may reach the skin through physical contact with the plant or, if the plant is eaten, the compound is absorbed unchanged from the digestive tract and transported in the circulatory system to peripheral areas of the skin (see Johnson, this proceedings). The photodynamic compound becomes phototoxic when activated by long-wave ultraviolet radiation of a suitable wavelength.

Light-skinned animals and birds are most prone to photosensitization. All areas not protected by hair, skin pigmentation, or feathers such as eyes, ears, nose, lips, vulva, and udder (in animals), and eyes, beak, wattle, comb, feet, and legs (in birds) may be severely burned (Williams and Binns 1968). Affected areas become erythemic, swell, crack, bleed, and eventually slough. Gangrene, sloughing of toes, comb, wattle, and eyelids, and crippling have been observed in poultry. Sloughing of hair and skin and deformities of the lips, ears, and eyes have been noted in photosensitized animals. Death rarely results directly from photosensitization, but may result from secondary causes such as infection of affected areas or starvation and dehydration resulting from the inability to locate food or water due to blindness or sealed eyelids.

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Species that evoke primary photosensitization are found primarily in the families Apiaceae, Rutaceae, Moraceae, Fabaceae, Hypericaceae, and Polygonaceae. Species most commonly associated with photosensitization in the United States are St. Johnswort (*Hypericum perforatum*) (family Hypericaceae) and buckwheat (*Fagopyrum sagittatum*) (family Polygonaceae) (Kingsbury 1964). The phototoxic compound in each species, hypericin and fagopyrin, respectively, has been isolated and named after the representative genus. Both compounds are naphthrodianthrone derivatives. Hypericin has been shown to have two action spectra, 540 M μ and 590 M μ ; the action spectrum of fagopyrin is 590 M μ . Buckwheat is a minor crop in the United States and cases of photosensitization from it are rare.

St. Johnswort is an introduced plant that has spread throughout the United States. It was the first plant to be identified as a primary photosensitizer. The plant became a major invader on California ranges where it adversely affected the sheep industry. A single dose of St. Johnswort at 5 percent of the body weight (calculated on a green weight basis) was phototoxic to sheep; 1 percent of the body weight was phototoxic to cattle. The beetle *Chrysolina quadrigemina*, introduced in 1946 for biological control, has reduced the infestation of St. Johnswort in California by about 99 percent.

The largest single group of compounds that cause primary photosensitization are the furocoumarins (psoralens). These compounds are found primarily in the Apiaceae and Rutaceae but are also found in two genera of the Fabaceae and one genus of the Moraceae (Pathak and others 1962). Primary photosensitization from furocoumarins in the United States is usually associated with members of the carrot family (Apiaceae). The furocoumarins are complex molecules that must have a specific configuration to be photoactive. Psoralen, bergapten, xanthotoxin, isoimperatorin, and bergamotin are highly phototoxic. Many other furocoumarins have no phototoxic properties.

PHOTOTOXICITY IN THE INTERMOUNTAIN WEST

Four highly phototoxic members of the Apiaceae are found in the Intermountain West: wild parsnip (*Pastinaca sativa*), cowparsnip (*Heracleum sphondylium*), spring parsley (*Cymopterus watsonii*), and a related species, *Cymopterus longipes*. Species of three other genera, *Angelica*, *Ligusticum*, and *Lomatium*, are phototoxic, but these species are not indigenous to the Intermountain

West. The foliage of cultivated parsnips, carrots, and celery is phototoxic and has evoked photosensitization in workers involved in their harvesting or processing.

Cymopterus longipes, a species common in pastures in northern Utah, does not produce phototoxic foliage, but does produce highly phototoxic seeds (Egyed and Williams 1977). The seeds contain the furocoumarin isoimperatorin.

Most livestock losses from photosensitization in the Intermountain West have been caused by spring parsley (Williams 1968). This small perennial grows in the early spring from southeastern Oregon and southwestern Idaho through Nevada to southwestern Utah. Spring parsley synthesizes the furocoumarins xanthotoxin and bergapten (Williams 1970). Xanthotoxin, which is five times more phototoxic than bergapten, occurs in greater concentrations. The appearance of the plant in southwestern Utah in late March and early April coincides with lambing. Ewes that graze the plant become photosensitized. Udders and teats become so inflamed and sensitive that the ewes refuse to let their lambs nurse. Losses of lambs from starvation and dehydration have run as high as 25 percent on some ranges in southwestern Utah and eastern Nevada.

Photosensitization in chicks fed leaves and seeds of spring parsley was characterized by erythema and swelling of scales on legs and feet, and acute erythema of the comb, beak, and eyelids. Young chicks were deformed after severe photosensitization (Van Kampen and others 1969). The upper beak failed to develop and was much shorter than the lower beak. The comb, wattle, eyelids, and other epidermal structures became gangrenous and sloughed after edema caused by the photosensitization disrupted blood circulation to those areas. Contracture of fibrous tissue in the legs resulted in deformities and sloughing of digits of the feet.

CONTROL METHODS

Spring parsley is the only primary photosensitizer in the Intermountain West for which a method of chemical control has been established (Williams and others 1970). Spring parsley was controlled 99 percent by one application of 2,4-D amine or ester applied at 2 lb/acre when plants were in early to late flower, usually from the middle of April to early May. These treatment dates are somewhat earlier than those recommended for control of big sagebrush (Artemisia tridentata); nevertheless, 2,4-D amine or ester usually controlled 50 to 70 percent of the adjacent big sagebrush when applied from the middle of April to early May.

Plots treated with 2,4-D were reevaluated three years after treatment to determine residual control of spring parsley. Little or no reinfestation occurred on these plots. Spring parsley was replaced primarily by ground smoke (Gayophytum diffusum) and common ragweed (Ambrosia

artemisiifolia). No increase in grasses was noted. Downy brome (Bromus tectorum), squirrel-tail (Sitanion hystrix), reverchon threeawn (Aristida glauca), and Indian ricegrass (Oryzopsis hymenoides) occurred on the plots but were generally located under or adjacent to big sagebrush. Although spring parsley produced seed abundantly each year, the plants did not establish readily from seed on the test site. Long-term control was possible, therefore, with one application of herbicide.

The phototoxicity of spring parsley decreased after application of 2,4-D amine or ester. Within 4 weeks after treatment the plants were not phototoxic at the highest rate (800 mg) that could be administered in a single dose to 1-week-old chicks, whereas 150 mg of the control plant was phototoxic.

REFERENCES

- Egyed, M. N.; Williams, M. C. Photosensitizing effects of Cymopterus watsonii and Cymopterus longipes in chickens and turkey poults. Avian Diseases. 21: 566-575; 1977.
- Kingsbury, J. M. Poisonous plants of the United States and Canada. Englewood Cliffs, NJ: Prentice-Hall; 1964. 626 p.
- Pathak, M. A.; Daniels, F., Jr.; Fitzpatrick, T. B. The presently known distribution of furocoumarins (psoralens) in plants. The Journal of Investigative Dermatology. 39: 225-239; 1962.
- Van Kampen, K. R.; Williams, M. C.; Binns, W. Deformities in chickens photosensitized by feeding spring parsley (Cymopterus watsonii). American Journal of Veterinary Research. 30: 1663-1665; 1969.
- Williams, M. C. Effects of herbicides on the capacity of spring parsley to photosensitize chickens. Weed Science. 16: 350-352; 1968.
- Williams, M. C. Xanthotoxin and bergapten in spring parsley. Weed Science. 18: 479-480; 1970.
- Williams, M. C.; Binns, W. Experimental photosensitization by spring parsley (Cymopterus watsonii) in chicks. American Journal of Veterinary Research. 29: 111-115; 1968.
- Williams, M. C.; Kreps, L. B.; Cronin, E. H. Control of spring parsley on rangeland. Weed Science. 18: 623-625; 1970.

A REVIEW OF PINE NEEDLE AND BROOM SNAKEWEED ABORTION IN CATTLE

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ABSTRACT: The ingestion of ponderosa pine (*Pinus ponderosa*) needles and broom snakeweed (*Gutierrezia microcephala* or *G. serotina*) results in significant losses each year to the cattle industry because of abortion and related complications. Pine-needle-induced abortion in cattle is predominantly a problem in the Western United States. Broom snakeweed causes significant losses in the Southwest; however, the plant is spreading northward and is found in most of the Western States, Mexico, and Canada. Abortions from pine needles and broom snakeweed are characterized by weak uterine contractions, early vulvar swelling, mucous or bloody discharge, premature udder filling, birth of small, weak or nonviable calves, abortion, retained placenta, and post-abortion toxemia. Death of the cow is common if treatment is not provided.

INTRODUCTION

Ponderosa pine (*Pinus ponderosa*) (fig. 1) grows in every State west of the great plains, in Western Canada, and is the State tree of Montana. It has a total stand greater than any native tree in the Western United States except Douglas-fir (*Pseudotsuga menziesii*). It grows at elevations between 5,000 and 8,000 feet, is drought resistant, and reaches a height of over 200 feet and is 5 to 8 feet in diameter under ideal environmental conditions. It is extensively harvested for lumber. During early growth the bark is dark brown to black, thus the name blackjack pine. Older trees develop a bark color of cinnamon brown to orange yellow. Other common names include western yellow pine, western soft pine, yellow pine, and bull pine (USDA 1949; Collingwood and Brush 1955). Ponderosa pine has needles 5 to 10 inches long growing in clusters of two to three. The cones are brown, 3 to 6 inches long, and frequently grow in clusters.

A partial nutrient composition of pine needles from two different areas in Wyoming revealed values comparable to those of low quality hay (table 1) (Hamilton and Miller 1956; Kamstra and Cogswell 1975).

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Figure 1.--Ponderosa pine (*Pinus ponderosa*) typical of the size often grazed by cattle (8 to 10 feet in height).

Table 1.--A partial nutrient composition of ponderosa pine needles

Nutrient	Unit	Amount
Carotene ¹	Mg/g	184.5
Ash ¹	Percent	2.4
Crude protein ¹	Percent	6.9
Ether extract ¹	Percent	12.1
N free extract ¹	Percent	46.3
Calcium ¹	Percent	0.34
Phosphorus ¹	Percent	0.15
Ca/P ratio ¹		2.3/1
Magnesium ¹	Percent	0.21
Manganese ¹	ppm	110.1
Nitrate ¹		Trace
Fiber content ²	Percent	28-35
Lignin ²	Percent	12-15
Digestibility ²	Percent	30-42

¹Taken from Hamilton and Miller (1956).

²Taken from Kamstra and Cogswell (1975).



Figure 2.--Broom snakeweed (Gutierrezia serotrhæ) in flower.

Broom snakeweed (Gutierrezia serotrhæ, fig. 2) is commonly called perennial snakeweed, slinkweed, turpentine weed, or matchbrush; and G. microcephala is called threadleaf broomweed. The two species are similar morphologically.

The snakeweeds are widely distributed in the Western United States, Mexico, and Canada. They extend from central Texas to California and from Saskatchewan, Canada, to northern Mexico (Lane 1985). They are widespread and invade depleted or disturbed rangeland excluding more palatable species (fig. 3). The snakeweeds are toxic to cattle, sheep, and goats. Abortion is a serious problem; losses occur every year (Mathews 1936; Dollahite and Anthony 1956; Dollahite and Anthony 1957; Dollahite and Allen 1959).

Snakeweeds are short-lived perennial shrubs ranging from 6 inches to 2 feet tall. Many unbranched erect stems originate from a woody base and die back when the plant enters dormacy. The leaves are narrow (1/8 to 1/4 inch wide) and 3/4 to 1-1/2 inches long. The flowers are yellow, in numerous clusters with three flowers per head in G. serotrhæ and one or two per head in G. microcephala. This is the distinguishing morphological difference between the two species (McDaniel and Loomis 1985).

The average life span of snakeweed is about 2.5 years (Parker 1982). Seedlings are sensitive to soil moisture, competition from other plants, and most die within the first year. Snakeweed rapidly increases in heavily overgrazed, burned, or disturbed sites and during and following drought. Its seeds germinate when favorable precipitation resumes and it rapidly increases as a result of reduced plant competition (Parker 1982).



Figure 3.--Heavy stands of broom snakeweed in New Mexico.

TOXICITY

Pine Needles

Primary toxicological effects of pine needles in cattle are abortion and complications associated with the abortion, such as retained placenta, metritis, toxemia, and death. Abortions in cows eating ponderosa pine needles generally occur in late fall, winter, and early spring. This time corresponds to when cows in most western cow-calf operations are in the third trimester of pregnancy and when cattle are most likely to graze pine needles (Stevenson and others 1972; James and others 1977). Abortions have been induced as early as 3 months gestation and have been reported by ranchers to occur anytime. However, the closer the ingestion of needles is to the time of normal parturition, the higher the incidence of abortion. Abortion may occur any time between 24 hours and 2 to 3 weeks following the ingestion of pine needles (Stevenson and others 1972; James and others in preparation). Abortions frequently occur following a single exposure to the needles (James and others 1977; Panter and others 1985), but results from controlled experiments indicate the highest incidence of abortion is in cows eating the needles over a period of days (James and others in preparation; Panter and others 1985). Abortions have been associated with grazing green needles from trees, slash from the lumber industry, and dead, dry needles from the ground (Stevenson and others 1972; James and others 1977). Other coniferous members of the pine family, spruces, junipers, and arbor-vitae may also cause toxic effects if grazed heavily (Tucker 1961; Muenscher 1975).

Usually cows do not graze pine needles, presumably because of their resinous taste and coarse texture, but under certain circumstances needles may be eaten heavily. A number of factors are believed to cause pregnant cows to graze pine needles. Those circumstances may be stress

related such as sudden weather changes that force cattle to seek the pine trees for shelter; lack of feed when cattle are hungry; changes to unfamiliar or poor quality feed; or sudden access to pine needles from windfalls or from lumbering operations; boredom or curiosity; and accidental ingestion with other feed (Stevenson and others 1972).

Abortions are characterized by weak uterine contractions, excessive uterine hemorrhage, incomplete dilation of the cervix, and often a characteristic nauseating odor. When cows graze needles over a period of time there is generally premature filling of the udder, early vulvar swelling, mucous or bloody discharge, abortion, birth of small weak calves, retained placenta, and post-abortion toxemia; death may occur (James and others 1977).

As the length of gestation increases, the vigor of the calf and the chance of survival increases. It appears that if the calf is delivered rapidly, early in the process of parturition, the calf's chance of survival is improved.

A persistent retained placenta is frequently observed regardless of the stage of gestation when the abortion occurs (Stevenson and others 1972). It has been observed that some herds of cattle that had access to pine needles, but did not abort, had a high incidence of retained placentas. Calves from these cows are often born small and weak and their survival rate is low. Some believe these calves are more susceptible to calfhood diseases.

Sheep, goats, and wildlife have been reported to abort from ingestion of pine needles (Stevenson and others 1972; McKnight 1985). However, research at our laboratory suggests that sheep are not as susceptible to the abortifacient effects of pine needles as cattle.

Toxic effects from pine needle extracts given to laboratory animals have been reported; however, toxic effects in livestock are equivocal. Pine needles fed to open cycling heifers were not toxic (Staigmiller and Panter 1985). The rapid death of many cows after abortion occurs suggests an acute toxemia resulting from the abortion and retained placenta.

The abortifacient agent(s) in pine needles are not known. Some researchers have suggested that mycotoxins may be the cause of the abortion (Chow and others 1974); others have suggested that ingestion of pine needles induces an infection with the microorganism *Listeria monocytogenes*, a known cause of abortion (Gray and Killinger 1966; Hether and others 1983; Hether and Jackson 1983; Adams and others 1979). Water-soluble fractions have been shown to cause resorption, stillborn kits, and reduced uterine growth in mice. The detrimental effect was lost when the aqueous fraction was autoclaved (Chow and others 1972). Similarly, pelleting of pine needles with steam eliminated the abortifacient effect of pine needles (Faulkner 1969). Cook (1960) reported that a water-soluble fraction of an acetone extract decreased the

uterine weight in immature female mice, but failed to cause reproductive dysfunction. Others reported complete reproductive failure from ingesting the pine needle residue after aqueous extraction, suggesting the presence of a water-insoluble toxin (Anderson and Lozano 1977). Wagner and Jackson (1983) reported a phytoestrogenic effect in pine needles that competed with 17- β estradiol for binding to mouse uterine cytosol. Embryonic resorptions were observed in mice after hexane extracts were administered early in gestation. The active components in this extract were isolated and identified as a mixture of diterpene resin acids that included pimaric, isopimaric, sandaracopimaric, palustric/lenopimaric, abietic, dehydroabietic, and neoabietic acid (Kubik and Jackson 1981). Anderson and Lozano (1979) reported a heat stable toxin soluble in methanol, ethanol, chloroform, hexanes, and 1-butanol that caused embryonic resorption in pregnant mice during the first 10 days of gestation. It is obvious from this short review that there is still much to be learned about the abortifacient element in pine needles, whether it be water soluble, water insoluble and heat stable, or heat labile.

Broom Snakeweed

Broom snakeweed causes abortion in cattle, sheep, and goats (Mathews 1936; Dollahite and Anthony 1956; Dollahite and Anthony 1957; Dollahite and Allen 1959). The abortion is similar to that from pine needles: premature udder development, early vulvar swelling, mucous and bloody discharge, abortion, birth of small weak calves, retained placenta, post-abortion toxemia, and death. There are, however, differences in toxicity. Broom snakeweed is toxic to cattle, sheep, and goats. Clinical signs of broom snakeweed toxicoses include anorexia, mucopurulent nasal discharge, crusted and sloughing skin and muzzle, listlessness, rough hair coat, hematuria, frequent painful urination, diarrhea in early stages followed by constipation, and large amounts of white mucous in foul smelling feces (Mathews 1936; Dollahite and Anthony 1956; Dollahite and Anthony 1957). The greatest losses occur from abortion in cattle. Mortality in cows is high if they do not receive supportive therapy.

Broom snakeweed varies in toxicity at different phenological stages and the site where it is growing. It is more toxic when growing rapidly, especially in the early stages of leaf growth. Although broom snakeweed grows abundantly on limestone soils, only sporadic losses are reported. Experiments have shown that abortions are much more prevalent when broom snakeweed grown on sandy soils is grazed (Dollahite and Anthony 1957).

The abortifacient and toxic elements in broom snakeweed have not been identified. Abortion and death were induced when saponins extracted from broom snakeweed were injected intravenously in cows, goats, and rabbits. Saponins administered orally to rabbits also caused abortion. However, a saponin from lechugilla (*Agave lecheguilla*),

known to be toxic, and a supposedly nontoxic, pharmaceutical-grade saponin produced abortion and death when administered intravenously to pregnant rabbits (Dollahite and others 1962; Shaver and others 1964). Molyneux and others (1980) identified the major mono terpenes and sesquiterpenes in the essential oil fraction of Cutierrezia sarothrae. These included alpha-pinene, myrcene, linalool, cis-verbenol, trans-verbenol, verbenone, geraniol, caryophyllene, and gamma-humulene.

ECONOMIC LOSSES

The actual economic losses from pine needle and broom snakeweed abortion and toxicity are not known, but losses occur in most areas where these plants grow. The incidence of abortion in an outbreak may vary from only a few to 100 percent. Mortality in cows is high if they do not receive supportive therapy.

Pine needle abortion occurs in the Western United States where heavy stands of ponderosa pine grow. Surveys conducted by the National Cattlemen's Association and others in the Black Hills area of South Dakota, Montana, and Wyoming suggest that pine needle abortion is a serious economic problem (Robinson 1984). In addition to the economic losses due to the abortions, the costs of management such as pruning, fencing cattle away from the pines, lost forage, supplemental feeding, increased veterinary care, and increased calving intervals must be considered. In an attempt to establish monetary losses from pine needle abortion, a Crook County, SD, survey estimated that \$700,000 was lost in one county from pine needle abortion (Robinson and Flinn 1984). This averaged over \$10,000 per rancher and included: abortions, calf losses, increased management to avoid pines, increased veterinary care for weak calves and sick cows, and increased feed supplementation. These estimates did not include the losses from increased calving intervals that carry over for several years, decreased production in the cow due to loss of condition, decreased lactation, or the losses from small, poor-growing calves. One can easily conclude that economic loss to the livestock industry from pine needles could amount to many millions of dollars annually.

Broom snakeweed is predominantly a problem in the Southwestern United States. In 1961 the annual loss to the livestock industry in Texas alone was estimated to be between \$2 and \$3 million (Dollahite and Anthony 1957). A more recent estimate (McGinty 1985) put the direct annual cattle losses attributable to broom snakeweed at over \$15 million. This does not include indirect losses such as underweights and loss of usable forage. If the losses occurring in New Mexico and Arizona were equal to this amount, then annual losses in the Southwest could exceed \$30 million (McGinty 1985).

A conservative estimate of the combined losses to the cattle industry due to ponderosa pine and broom snakeweed is \$40-50 million annually.

METHODS OF CONTROL

Ponderosa pine is important to the lumber industry. Methods of control have not been extensively studied. Suggested methods of control include clear-cutting stands in areas where cattle graze the needles, controlled burning, and experimental spraying. Spraying has been used on an experimental basis to keep young stands of pines from encroaching onto rangelands, but no methods of treatment have been published or recommended. Generally, management methods such as fencing pregnant cows away from the pines and supplemental feeding practices are used to reduce losses from pine needles.

For broom snakeweed, methods of control have been tested. One method is to apply 2,4-D at a rate of 1 lb/acre for 2 successive years. Significant control requires good soil moisture and growing conditions present (Sperry and Robinson 1963). Picloram has been effective when applied at rates ranging from 0.25 to 1 lb/acre for pellets and liquid (Schmutz and Little 1970; Gesink and others 1973). More recently low rates of picloram in combination with other herbicides have proven effective and less expensive. Picloram at 0.25 lb/acre in combination with 2,4-D at 1 lb/acre, or in combination with tryclopyr at 0.4 lb/acre, or in combination with dicamba at 0.25 lb/acre has produced kill rates greater than 95 percent (Jacoby and others 1982; Sosebee and others 1982a). A good kill rate can be obtained any time the plant is actively growing, but best results have been obtained at the end of the flowering period (Sosebee and others 1982b).

REFERENCES

- Adams, C. J.; Neff T. E.; Jackson, L. L. Induction of Listeria monocytogenes infection by the consumption of ponderosa pine needles. *Infection and Immunity*, 25(1): 117-120; 1979.
- Anderson, C. K.; Lozano, E. A. Pine needle toxicity in pregnant mice. *Cornell Vet.* 67: 229-235; 1977.
- Anderson, C. K.; Lozano, E. A. Embryotoxic effects of pine needles and pine needle extracts. *Cornell Vet.* 69: 169-175; 1979.
- Chow, F. C.; Hamar, D. W.; Udall, R. H. Mycotoxic effect on fetal development: Pine needle abortion in mice. *J. Reprod. Fert.* 40: 203-204; 1974.
- Chow, F. C.; Hanson, K. J.; Hamar, D. W., and others. Reproductive failure of mice caused by pine needle ingestion. *J. Reprod. Fert.* 30: 169-172; 1972.
- Collingwood, G. H.; Brush, W. D.: *Knowing your trees*. Washington, DC: The American Forestry Association; 1955: 20-21.

- Cook, H. The effects of birdsfoot trefoil and yellow pine needles on the reproductive process of the laboratory mouse and rat. Vancouver, BC: University of British Columbia; 1960. 75 p. Thesis.
- Dollahite, J. W.; Allen, T. J. Feeding perennial broomweed to cattle, swine, sheep, goats, rabbits, guinea pigs and chickens. Progress Report 2105. College Station, TX: Texas Agricultural Experiment Station; 1959: 1-6.
- Dollahite, J. W.; Anthony, W. V. Experimental production of abortion, premature calves and retained placentas by feeding a species of perennial broomweed. South Western Veterinarian. 1956 Winter: 128-131.
- Dollahite, J. W.; Anthony, W. V. Poisoning with Gutierrezia microcephala a perennial broomweed. J. Am. Vet. Med. Assoc. 130(12): 525-530; 1957.
- Dollahite, J. W.; Shaver, T.; Camp, B. J. Injected saponins as abortifacients. J. Am. Vet. Res. 23: 1261-1263; 1962.
- Faulkner, L. C. Pine needle abortion. In: Faulkner, L. C., ed. Abortion diseases in livestock. Springfield, IL: Charles C. Thomas; 1969: 75-79.
- Gesink, R. W.; Alley, H. P.; Lee, G. A. Vegetative response to chemical control of broom snakeweed on a blue grama range. J. Range Manage. 26: 139-143; 1973.
- Gray, M. L.; Killinger, A. H. Listeria monocytogenes and listeric infections. Bact. Rev. 30: 309-382; 1966.
- Hamilton, J. W.; Miller, G. J. A chemical study of Pinus ponderosa needles in relation to poisoning cattle. Quarterly Report No. 653. Laramie, WY: Wyoming Agricultural Experiment Station; 1956.
- Hether, N. W.; Campbell, P. A.; Baker, L. A., and others. Chemical composition and biological functions of Listeria monocytogenes cell wall preparations. Infection and Immunity. 39(3): 1114-1121; 1983.
- Hether, N. W.; Jackson, L. L. Lipoteichoic acid from Listeria monocytogenes. J. Bact. 156(2): 809-817; 1983.
- Jacoby, P. W. Jr.; Meadows, C. H.; Foster M. A., and others. Control of broom snakeweed (Xanthocephalum sarothrae) with fall application of foliar herbicides. Progress Rep. 4031. College Station, TX: Texas Agricultural Experiment Station; 1982. 5 p.
- James, L. F.; Call, J. W.; Stevenson, A. H. Experimentally induced pine needle abortion in range cattle. Cornell Vet. 67(2): 293-299; 1977.
- James, L. F.; Panter, K. E., Call, J. W., and others. Pine needle abortion in cattle: A review and report on recent research. [In preparation] Logan, UT; U.S. Department of Agriculture, Agriculture Research Service, Poisonous Plant Research Laboratory; 1986. 10 p.
- Kamstra, L. D.; Cogswell, C. Pine needle abortion among cows grazing foothill ranges. A.S. Series 75-44. Brookings, SD: South Dakota Agricultural Experiment Station; 1975: 48-50.
- Kubik, Y. M.; Jackson, L. L. Embryo resorptions in mice induced by diterpene resin acids of Pinus ponderosa needles. Cornell Vet. 71(1): 34-42; 1981.
- Lane, M. Taxonomy of Gutierrezia Lag. (Compositae: Astereae) in North America. Systemic Botany 10(1): 7-28; 1985.
- Mathews, F. P. The toxicity of broomweed (Gutierrezia microcephala) J. Am. Vet. Med. Assoc. 41(1): 55-61; 1936.
- McDaniel, K. C.; Loomis, L. E. Livestock poisoning by perennial snakeweeds. Weeds Today, 16(1): 9-11; 1985.
- McGinty, A. Survey suggests broomweed costs far more than previously thought. Livestock Weekly. 1985 September 5 and 6.
- McKnight, A. Personal communication. 1985. Fort Collins, CO: Colorado State University, Department of Veterinary Science.
- Molyneux, R. J.; Stevens, K. L.; James, L. F. Chemistry of toxic range plants: volatile constituents of broomweed (Gutierrezia sarothrae). J. Agric. Food Chem. 28: 1332-1333; 1980.
- Muenschner, W. C. Poisonous plants of the United States. New York: Macmillan Publishing; 1975. 277 p.
- Panter, K. E.; Staigmiller, R. B.; James, L. F., and others. Abstract: 6th annual food animal veterinary conference, 1985 March 18-20; Logan, UT: Utah State University; 1985. p 44.
- Parker, M. A. Association with mature plants protects seedlings from predation in an arid grassland shrub (Gutierrezia microcephala). Oecologia. 53: 276-280; 1982.
- Robinson, J. Personal communication. 1984. New Castle, SD.
- Robinson, J.; Flinn, L. D. Pine needle abortion survey. New Castle, SD: South Dakota State Extension Service; 1984. 3 p.
- Schmutz, E. M.; Little, D. E. Effects of 2,4,5-T and picloram on broom snakeweed in Arizona. J. Range Manage. 23: 354-357; 1970.

- Shaver, T. N.; Camp B. J.; Dollahite, J. W. Ann. New York Acad. Sci. 111: 737-743; 1964.
- Sosebee, R. E.; Seipp, W. W.; Bedunah, D. J., and others. Herbicide control of broom snakeweed. Lubbock, TX: Texas Tech, Range and Wildlife Department. Noxious Brush and Weed Control Research Highlights. 13: 18; 1982a.
- Sosebee, R. E.; Seipp, W. W.; Alliney, J. Effect of timing of herbicide application on broom snakeweed control. Lubbock, TX: Texas Tech, Range and Wildlife Department. Noxious Brush and Weed Control Research Highlights. 13: 19; 1982b.
- Sperry, O. E.; Robinson, E. D. Chemical control of perennial broomweed. Prog. Rep. 2273. College Station, TX: Texas Agricultural Experiment Station; 1963. 7 p.
- Staigmiller, R. B.; Panter, K. E. Pine needle abortion in beef cattle. Biol. Rep. 32: Suppl. 1; 148; 1985.
- Stevenson, A. H.; James, L. F.; Call, J. W. Pine-needle (Pinus ponderosa) induced abortion in range cattle. Cornell Vet. 62(4): 519-524; 1972.
- Tucker, J. S. Pine needle abortion in cattle. Proc. Am. Coll. Vet. Tox. St. Louis, MO: 35-39; 1961.
- U.S. Department of Agriculture. Trees. Yearbook of Agriculture. Washington, DC: U.S. Department of Agriculture; 1949: 71.
- Wagner, W. D.; Jackson, L. L. Phytoestrogen from Pinus ponderosa assayed by competitive binding with 17β -Estradiol to mouse uterine cytosol. Theriogenology. 19(4): 507-516; 1983.

Section 4. Foraging Behavior

DIET TRAINING: BEHAVIORAL CONCEPTS AND MANAGEMENT OBJECTIVES

Frederick D. Provenza and David F. Balph

ABSTRACT: Diet training is the manipulation of livestock dietary habits to meet a management objective. We believe diet training has the potential for making livestock production more efficient and rangelands more productive for livestock. This paper briefly describes some behavioral concepts underlying diet training and outlines potential management objectives for livestock and rangelands. These objectives include training young animals: (1) to recognize, readily accept, and efficiently harvest foods that they will encounter later in life; (2) to avoid desirable or poisonous plants; and (3) to better accept plants that have low palatability.

INTRODUCTION

Commercial success is determined by the relationship between production costs and prices received for a product. Livestock producers have relatively little control over the prices they receive for animals but can manage costs. Economic survival when profit margins are low, as they often are, necessitates a search for economical operations.

Diet training of livestock is a developing concept that may be useful in reducing costs of raising livestock. Diet training is the manipulation of an animal's dietary habits to meet a management objective. Elsewhere, we present theoretical arguments and empirical evidence supporting the concept as well as some inherent constraints on diet manipulation (Provenza and Balph in press). This paper reviews (1) behavioral principles upon which this type of management is based and (2) potential management objectives.

FEASIBILITY OF DIET TRAINING

Role of Learning

Natural selection matches an animal to its environment. This match with respect to foraging behavior of livestock probably still exists, because domestication has resulted in more quantitative than qualitative changes (Price 1984). Generalist herbivores such as livestock

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encounter a variety of potential foods on rangelands, some of which are appropriate while others are not. We believe the difficulty in discriminating among forages gives a selective advantage to animals whose diet selection is based on generality and flexibility. Learning what to eat and what to avoid provides generality and flexibility.

Evidence that ungulates learn what and what not to eat comes from a variety of sources. For example, animals of the same species reared in different habitats often prefer different foods when foraging in the same habitat (Arnold 1964; Leuthold 1971; Arnold and Maller 1977; Martin 1978; Frost 1981; Bartmann and Carpenter 1982). Sheep not only select foods based on their taste and texture, but also prefer foods that they can ingest quickly (Kenney and Black 1984), a factor that is probably also governed by learning. Livestock can also learn to avoid palatable foods that make them sick (Zahorik and Houpt 1977, 1981; Thorhallsdottir and others in press). These studies suggest that food habits are modified by past experience rather than determined by a presumption strategy based on energy or nutrient gain (Pyke 1984; Krebs and McCleery 1984).

Animals feeding on known foods in familiar settings (for example sheep: Arnold 1970; Arnold and Maller 1977; goats: Provenza and Malechek in press; cattle: Hodgson 1971; Hodgson and Jamieson 1981) spend less time, and hence energy (Osuji 1974), foraging but ingest more food than inexperienced animals. These differences in foraging efficiency, which persisted for as long as trials were conducted, in some cases 10 months, suggest that learning may affect foraging skills as well as food recognition and acceptance.

Learning Efficiency

The use of social models to shape dietary habits of young livestock may increase learning efficiency. Social learning may help an inexperienced animal learn from an experienced animal, thus avoiding the inefficiency and risk of testing everything itself. Social learning theory (Bandura 1977; Boyd and Richerson 1985) predicts that the best models are nurturants and respected peers. The genetic relationship between a mother and her young means that they should respond similarly to cues provided by, and consequences associated with, foods. The mother might also influence food habits of her young by transmitting odors and tastes from foods through her milk (Galef 1976; Madsen 1977).

The evidence that social learning may be important to livestock comes from recent studies of sheep. Ewes apparently influence lambs' consumption of molasses-urea blocks (Lobato and others 1980) and whole-grain wheat supplements (Lynch and others 1983; Green and others 1984). Our research (Thorhallsdottir and others 1986) suggests that young lambs exposed to foods with their mothers consume about twice as much of the same foods after weaning as do lambs exposed with an adult ewe that is not their mother. Lambs exposed with an adult ewe consume about twice as much of the foods as do lambs exposed alone. Lambs allowed to eat the foods during exposure consume about twice as much of the foods after weaning as do lambs that only observe the foods or the mother or another adult ewe eating the foods.

Food imprinting, should it exist, may also increase learning efficiency. Imprinting is a type of learning that occurs during a sensitive period; the behavior learned during this period persists throughout life (reviewed by Hess 1973; Immelmann 1975). Imprinting helps an animal acquire important information during a specific time. Should food imprinting occur in livestock, diet training could be brief and animals would remember what they have learned. The sensitive period may be during weaning (Martin 1984). During weaning the developing animal must make the major transition from complete dependence on maternal care to independence (Galef 1981). Young herbivores initially learn about foods during this period, and can learn from their mothers. The age at which young are weaned naturally depends on the nutritional status of the mother (Arnold and others 1979), and the sensitive period may coincide with the weaning period rather than a specific age.

Limited evidence suggests that young animals learn about foods more readily than older animals, but little empirical evidence exists to suggest that the phenomenon is food imprinting. Arnold and Maller (1977) found that sheep from different environments persistently selected diets of different botanical composition, and that dietary experiences in early life had more effect on later dietary habits than when these experiences occurred at older ages. Further, Lobato and others (1980) found that sheep ate molasses-urea blocks if they had been exposed to them as lambs before about 9 months age suggesting a sensitive period. Lynch and others (1983), however, were unable to detect any difference in the response of lambs exposed to whole-grain wheat at different ages during the first 11 weeks of life. Finally, we exposed lambs as (1) monogastrics, (2) during weaning, and (3) as ruminants to the shrub Cercocarpus montanus (Squibb and others 1986). Our results are consistent with the hypothesis that a sensitive period for learning occurs during weaning, but do not rule out other explanations.

LIVESTOCK PRODUCTION OBJECTIVES

If learning affects food recognition and ingestion rates, animals such as replacement females which are reared in one environment and moved to new environments where the physical and chemical characteristics of foods are unfamiliar may forage inefficiently; they are forced to relearn what and how to eat (Zimmerman 1980). Exposing young animals to foods they will encounter later in life could increase livestock performance and thereby reduce costs. Such training might also enhance intake of supplements such as protein blocks, shrubs on grass-shrub pastures (Gade and Provenza in press), or rations in feedlots.

Animals moved to new environments also encounter unfamiliar poisonous plants and may be more vulnerable to those plants than animals familiar with them (Behnke 1980). Losses caused by poisonous plants might be reduced if we better understood how livestock detect and avoid toxic plants, and if young livestock could be trained to avoid harmful plants that are highly palatable or contain slow-acting poisons. To date, however, little research on this topic has been conducted with domestic livestock.

Most research on learned food aversions has been conducted by psychologists studying rats (Braveman and Bronstein 1985). Rats are capable of discovering a harmful food up to 12 hours after ingesting a meal of several items, only one of which was harmful (Rozin 1976). Rats respond to novel foods or foods eaten in novel places by periodically sampling the item and eating increasing amounts as long as they experience no adverse consequences. If they become ill, they immediately avoid the novel food and eat only what has been safely consumed in the past.

Ruminants may or may not fit the rat taste aversion model. As generalist herbivores, they also encounter noxious foods. Ruminants, however, have complex stomachs and may sense gastronomic distress differently from rats. Ruminants also ingest many foods during long periods of foraging, which may make it more difficult for them to discover if a food is harmful. Published literature on this topic indicates that livestock can be trained to avoid certain foods if they are simultaneously given lithium chloride (LiCl), a gastrointestinal poison (Zahorik and Houpt 1977, 1981). Our research (Thorhallsdottir and others in press) on learned food aversions suggests that sheep persistently avoid palatable foods containing LiCl; however, they sample small quantities of foods associated with illness and increase consumption when ingestion is no longer paired with illness. Additional research is required to fully determine the learning abilities of livestock and evaluate the potential management value of conditioned food aversions.

RANGE MANAGEMENT OBJECTIVES

Rangelands contain many kinds of plants, some preferred more than others by livestock. Traditionally, ranges are improved by reducing the abundance of less preferred species and planting more preferred species (reviewed by Vallentine 1971). Rather than directing all our efforts at improving rangelands for livestock, perhaps we could better match the foraging behavior of livestock to rangelands.

Selective grazing of preferred plant species by livestock can cause undesirable changes in soil stability and plant composition on rangeland (Stoddart and others 1975). To the degree that livestock can be conditioned to increase consumption of less palatable and weedy species, undesirable changes in soils and vegetation can be mitigated. Increasing utilization of less desirable species by even 10 to 20 percent might prevent, or at least delay, such changes.

Conversely, diet training might be used to prevent livestock from eating plant species desirable to foresters. Livestock grazing in forest plantations can enhance tree seedling growth and survival, but livestock often consume tree seedlings along with herbaceous species (Hsieh 1985). Aversive conditioning might be used to train young livestock to avoid tree seedlings.

Finally, managers base the carrying capacity of rangeland on the distribution of animals, and broad distribution of livestock is essential for effective use of the forage resource (Cook 1967). Learning may affect habitat selection (Hunter and Milner 1963; Cook 1967) as well as dietary habits. If so, it may be possible to train livestock to use a greater proportion of the range. Such training would enhance use of the forage resource and thereby increase carrying capacity. In addition, it may be possible to teach livestock to seek out and use sections of the range differentially. Such training could be used to increase use of upland, as opposed to riparian habitats, an important management objective in areas of the western United States where excessive use of riparian areas by livestock causes degradation of fishery resources.

CONCLUSIONS

We believe learning plays a fundamental role in the development of an herbivore's dietary habits. The likelihood that livestock learn to forage presents both problems and opportunities to livestock producers and range managers. Learning may result in inefficient or inappropriate foraging when animals are moved to new environments. Conversely, the manipulation of dietary experience may let a manager create a foraging group better suited to specific management goals.

REFERENCES

- Arnold, G. W. Some principles in the investigation of selective grazing. *Proc. Aust. Soc. Anim. Prod.* 5: 258-271; 1964.
- Arnold, G. W. Regulation of food intake in grazing ruminants. In: Phillipson, A. T., ed. *Physiology of digestion and metabolism in the ruminant*. London: Oriel Press; 1970: 264-276.
- Arnold, G. W.; Maller, R. A. Effects of nutritional experience in early and adult life on the performance and dietary habits of sheep. *Appl. Anim. Ethol.* 3: 5-26; 1977.
- Arnold, G. W., Wallace, S. R.; Maller, R. A. Some factors involved in natural weaning processes in sheep. *Appl. Anim. Ethol.* 5: 43-50; 1979.
- Bandura, A. *Social learning theory*. Englewood Cliffs, NJ: Prentice-Hall; 1977. 247 p.
- Bartmann, R. M.; Carpenter, L. H. Effects of foraging experience on food selectivity of tame mule deer. *J. Wildl. Manage.* 46: 813-818; 1982.
- Behnke, R. H. *The herders of Cyrenaica: ecology, economy, and kinship among the Bedouin of eastern Libya*. Chicago: University of Illinois Press; 1980. 197 p.
- Boyd, R.; Richerson, P. J. *Culture and the evolutionary process*. Chicago: University of Chicago Press; 1985. 331 p.
- Braveman, N. S.; Bronstein, P., eds. *Experimental assessments and clinical applications of conditioned food aversions*. New York: New York Academy of Science; 1985. 441 p.
- Cook, C. W. Increased capacity through better distribution on mountain ranges. *Utah Farm Home Science* 2: 39-42; 1967.
- Frost, S. K. Food selection in young naive impala *Aepyceros malampus*. *South African J. Zool.* 16: 123-124; 1981.
- Gade, A. E.; Provenza, F. D. Nutrition of sheep grazing crested wheatgrass versus crested wheatgrass shrub pastures during winter. *J. Range Manage.* [In press].
- Galef, B. G., Jr. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In: Rosenblatt, J. S.; Hinde, R. A.; Shaw, E.; Beer, C. eds. *Advances in the study of behavior*. Vol. 6. New York: Academic Press; 1976: 77-100.

- Galef, B. G. Jr. The ecology of weaning: parasitism and the achievement of independence of altricial mammals. In: Gubernick, D. J.; Klopfer, P. H. eds. Parental care in mammals. New York: Plenum Press; 1981: 211-241.
- Green, G. C.; Elwin, R. L.; Mottershead, B. E.; Keogh, R. G.; Lynch, J. J. Long term effects of early experience to supplementary feeding in sheep. Proc. Aust. Soc. Anim. Prod. 15: 373-375; 1984.
- Hess, E. H. Imprinting. New York: Van Nostrand Reinhold; 1973. 488 p.
- Hodgson, J. The development of solid food in calves. I. The effects of previous experience of solid food, and the physical form of the diet, on the development of food intake after weaning. Anim. Prod. 13: 15-24; 1971.
- Hodgson, J.; Jamieson, W. S. Variations in herbage mass and digestibility, and the grazing behaviour and herbage intake of adult cattle and weaned calves. Grass and Forage Sci. 36: 39-48; 1981.
- Hsieh, C. H. Cattle grazing in forests: a review relevant to conditions in Taiwan. Logan, UT: Utah State University; 1985. 74 p. Thesis.
- Hunter, R. F.; Milner, C. The behaviour of individual, related and groups of South Country Cheviot Hill sheep. Anim. Behav. 11: 507-513; 1963.
- Immelmann, K. Ecological significance of imprinting and early learning. Annu. Rev. Ecol. Syst. 6: 15-37; 1975.
- Kenney, P. A.; Black, J. L. Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. Aust. J. Agric. Res. 35: 551-563; 1984.
- Krebs, J. R.; McCleery, R. H. Optimization in behavioral ecology. In: Krebs, J. R.; Davies, N. B. eds. Behavioural ecology. 2d ed. Sunderland, MD: Sinauer Associates; 1984: 91-121.
- Leuthold, W. A note on the formation of food habits in young antelopes. East African Wildl. J. 9: 154-156; 1971.
- Lobato, J. F. P.; Pearce, G. R.; Beilharz, R. G. Effect of early familiarization with dietary supplements on the subsequent ingestion of molasses-urea blocks by sheep. Appl. Anim. Ethol. 6: 149-161; 1980.
- Lynch, J. J., Keogh, R. G.; Elwin, R. L.; Green, G. C.; Mottershead, B. E. Effects of early experience on the post-weaning acceptance of whole grain wheat by fine-wool merino lambs. Anim. Prod. 36: 175-183; 1983.
- Madsen, F. C. Flavoring agent transmits feed preference. Anim. Nutr. Health. 32: 15-16; 1977.
- Martin, G. C. The animal-plant complex in forage palatability phenomena. J. Anim. Sci. 46: 1470-1477; 1978.
- Martin, P. The meaning of weaning. Anim. Behav. 32: 1257-1259; 1984.
- Osuji, P. O. The physiology of eating and the energy expenditure of the ruminant at pasture. J. Range Manage. 27: 437-443; 1974.
- Price, E. O. Behavioral aspects of animal domestication. Q. Rev. Biol. 59: 1-32; 1984.
- Provenza, F. D.; Balph, D. F. Diet learning by domestic ruminants: theory, evidence, and practical implications. Appl. Anim. Behav. Sci. [In press].
- Provenza, F. D.; Malechek, J. C. A comparison of food selection and foraging behavior in juvenile and adult goats. Appl. Anim. Behav. Sci. [In press].
- Pyke, G. H. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. 15: 523-575; 1984.
- Rozin, P. The selection of foods by rats, humans and other animals. In: Rosenblatt, J. S.; Hinde, R. A.; Shaw, E.; Beer, C., eds. Advances in the study of behavior. Vol. 6. New York: Academic Press; 1976: 21-76.
- Stoddart, L. A.; Smith, A. D.; Box, T. W. Range management. New York: McGraw-Hill; 1975. 532 p.
- Squibb, R. C.; Provenza, F. D.; Balph, D. F. Development of a feeding response to Cercocarpus montanus in orphan lambs. Abstracts 39th annual meeting, Society for Range Management; Orlando-Kissimmee, FL, Denver, CO: Society for Range Management; 1986: Abstract No. 404.
- Thorhallsdottir, A. G.; Provenza, F. D.; Balph, D. F. Role of social models in the development of dietary habits of lambs. Unpublished data on file at Range Science Department, Utah State University; Logan, UT; 1986.
- Thorhallsdottir, A. G.; Provenza, F. D.; Balph, D. F. Food aversion learning in sheep. Appl. Anim. Behav. Sci. [In press].
- Vallentine, J. F. Range development and improvements. Provo, UT: Brigham Young University Press; 1971. 516 p.

Zahorik, D. M.; Houpt, K. A. The concept of nutritional wisdom: applicability of laboratory learning models to large herbivores. In: Barker, L. M.; Best, M.; Domjam, M. eds. Learning mechanisms in food selection. Baylor, TX: Baylor University Press; 1977: 45-67.

Zahorik, D. M.; Houpt, K. A. Species differences in feeding strategies, food hazards, and the ability to learn food aversions. In: Kamil, A. C.; Sargent, T. D., eds. Foraging behavior: ecological, ethological, and psychological approaches. New York: Garland; 1981: 289-310.

Zimmerman, E. Desert ranching in central Nevada. Rangelands. 2: 184-186; 1980.

DOMESTIC HERBIVORE FORAGING TACTICS AND LANDSCAPE PATTERN

R. L. Senft

ABSTRACT: This paper outlines a conceptual model of large herbivore interactions with vegetation pattern. Foraging decisions by large generalist herbivores aggregate into characteristic patterns at landscape and plant community levels. At the landscape level, domestic herbivores select plant communities and certain topographic zones as feeding areas. Community preference (percent feeding time/percent pasture area) follows a modified matching pattern and is directly proportional to relative biomass of preferred plant species. At community and individual plant levels, species preference (percent in diet/percent in herbage) is an exponential function of relative palatability, where palatability is loosely correlated with nutritive quality and/or presence of phytochemical deterrents. This is an overmatching pattern (Staddon 1983) as animals exhibit a disproportionate response to selection cues.

INTRODUCTION

What are general patterns of plant-herbivore interactions? What aspects of the forage environment provide relevant cues for habitat and diet selection? What "rules" do herbivores use to select food items? These questions are of practical as well as theoretical interest. Understanding plant-herbivore interactions would allow prediction of animal foraging behavior under a variety of management regimens and in a wide range of vegetation types. Further, elucidation of basic patterns of herbivore foraging would provide a framework within which the influence of plant secondary compounds could be evaluated.

A model of foraging behavior should include units of selection, plausible currencies and rules for discriminating among feeding options in a complex forage environment. A rudimentary model of plant-herbivore interactions is proposed. Although formulated at the level of foraging patterns (i.e., averages of many individual foraging decisions), the model may be elaborated to describe interactions with chemically complex vegetation. Further, the model may serve as a guide for predicting animal responses to changes in plant communities and to landscape-level pattern.

HIERARCHICAL FOOD RESOURCES

Vegetation may be viewed as hierarchically structured (Forman and Godron 1981). Although levels are to some extent observer-defined (Allen and Starr 1982), hierarchy concepts can provide a framework for dealing with ecological complexity in ways relevant to foraging behavior. In wildland ecosystems, individual plants aggregate in conjunction with soils to form plant communities, boundaries of which may be gradual or sharply defined. At a higher level of organization, soil-plant associations aggregate with landforms to form landscape systems (Forman and Godron 1981). For our purposes boundaries of a landscape system will be the limits of movement of an ungulate herd for some reasonable length of time. For domestic herds these boundaries may coincide with fences or be defined by home range behavior (Hunter 1964). At the lower end of the scale, plants themselves are hierarchically structured in ways relevant to animal nutrition and feeding behavior.

Large herbivore foraging behavior assumes different forms at different levels of the ecological hierarchy (table 1). The relevant response at a given level is preference for units comprising the next lower level. Selection of preferred feeding areas within the home range occurs at the landscape level, units of selection being plant communities or terrain types. Diet selection occurs at both plant community and individual plant levels, involving discrimination among individual plants and plant parts.

COMMUNITY-LEVEL FORAGING

Diet selection in large herbivores is based in large part on palatability of plant species and plant parts (Heady 1964). Palatability is loosely correlated with nutritive quality and may be modified by plant physical characteristics, presence of secondary compounds, and prior feeding experience. In fairly simple vegetation types, relative species preference (RP = percent in diet/percent in herbage) may be an exponential function of relative nutritive quality (RNQ):

$$RP = c \cdot \prod_i (RNQ_i - 1)$$

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where k is a selectivity coefficient (Senft 1984). RNQ is the ratio of a positive nutritional currency in item i to the mean level in the community:

$$RNQ_i = \frac{x_i}{\sum_{j=1}^n b_j \cdot x_j}$$

where x is concentration of the nutrient and b is proportional biomass of a food item.

Where secondary compounds provide strong negative signals to diet selection, RP may be a negative exponential function of concentration (see other papers in this volume). Therefore, species preference may be better expressed as an exponential function of palatability rather than of nutritive quality. Palatability in this case may be a multivariate function of physical and chemical characteristics. For modeling purposes, it may be convenient to represent intrinsic palatabilities as dimensionless numbers derived from field or laboratory trials (Senft and others 1986).

Disproportionate preference for relatively nutritious items results in diets being higher in nutritive quality than the herbage on average. Exponential selection response to nutritive quality may thus result in a nutrient maximization pattern (Belovsky 1984). This is not a strict maximization response as low quality or peripheral diet items may make up significant proportions of the diet due to high relative availability. Further, nutritive properties of some items may be masked by unpalatable secondary compounds (Provenza and Malechek 1984), resulting in an apparent strategy of minimization of toxic compounds.

LANDSCAPE-LEVEL FORAGING

Large herbivores interact with landscape pattern through selection of feeding areas. In arid and semi-arid regions, domestic herbivores frequent mesic lowlands and drainages due in part to location of preferred plants and to herbage response to soil moisture (Culley 1938; Moorefield and Hopkins 1951; Peterson and Woolfolk 1955). In forested areas, grazers may concentrate on open meadow communities (Senft 1986). Browsers, on the other hand, may concentrate on patches in which preferred woody species are abundant (Hanley 1984). Correlational studies have suggested that preference for plant communities (RCP) is a linear function of relative abundance and(or) nutritive quality of food plants (Hunter 1962; Hanley 1984; Senft and others 1985; Senft 1986). This response is similar to Herrnstein's (1970) matching law, an aggregate pattern in which relative feeding effort is proportional to relative reward. Herrnstein's model can be readily modified to describe landscape level foraging patterns by:

$$RCP_i = \frac{G_i}{A_i} = \frac{B_i}{\sum_{j=1}^n \frac{A_j B_j}{B_j}}$$

where G is the proportion of total grazing time spent in a community, B is absolute biomass (kg/ha) of preferred plants and A is proportional area of a community. The quantity on the left side of the matching equation is community preference, that on the right side is relative biomass availability. To account for the effects of nutritive quality or palatability, biomass of individual species may be weighted by palatability ratios. It should be noted that the matching model describes community use as a function of a foraging currency; modifying terms must be added to account for factors such as topography or proximity to a watering point (Senft and others 1985). Nonetheless, this model may describe community use in widely divergent vegetation types (fig. 1).

IMPLICATIONS

An unexpected result of large herbivore foraging rules is an indirect relationship between preference and relative availability. In a hypothetical community composed of a palatable and an unpalatable plant, preference for either species is related to relative contribution to the herbage (dotted lines in fig. 2a). Accordingly, species preferences show wide variation when items are rare and converge to neutrality (RP approaches 1.0) when common (points in fig. 2a). A

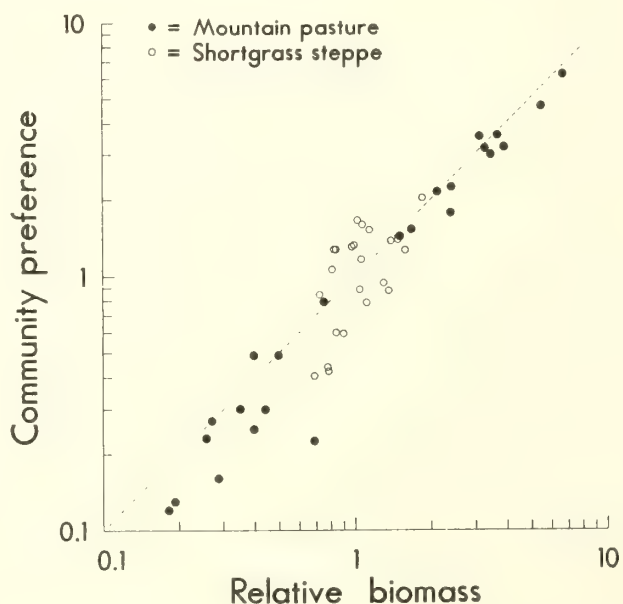


Figure 1.-- Relationship between relative community preference in cattle and relative graminoid biomass on shortgrass steppe and forested mountain pastures (Senft and others 1985; Senft 1986).

similar relationship is found between community preference and relative area (percent of total pasture area) (fig. 2b). Because of the exponential nature of the species selection rule the range in species preferences is wider than that observed for community preference.

The hierarchical foraging model may be useful in predicting large herbivore exploitation of landscape mosaics containing plants bearing anti-herbivore chemistry and the role of herbivores in succession in vegetation types where phytochemical deterrents are important. The main consequence of the community-level availability effect (fig. 2a) is that unpalatable plants will be strongly avoided until they comprise a majority of available forage in a community. At the landscape level, communities with large proportions of unpalatable plants will be avoided in favor of communities with large proportions of palatable plants. Since animals respond primarily to biomass of preferred plants, this would hold true even if the total biomass in the community comprised of palatable plants were less than that in the community comprised of unpalatable plants (see Hunter 1962). Thus, there would be strong tendency for animals to utilize plants without phytochemical deterrents, particularly in communities dominated by palatable species. The net effect would be to push the composition of plant communities and of the landscape system towards dominance by plants bearing secondary compounds (see related papers in this volume). Thus, as palatable plants become increasingly rare, pressure by herbivores will increase, thereby accelerating successional trend.

CONCLUSION

The foregoing suggests that there may be basic forms or patterns to plant-herbivore interactions that are independent of vegetation type and perhaps general across species. Patterns of interaction differ with level of ecological organization. Yet, there are underlying similarities in the basic type of response (preference) and in relativistic nature of foraging currencies. Further, although details of interactions

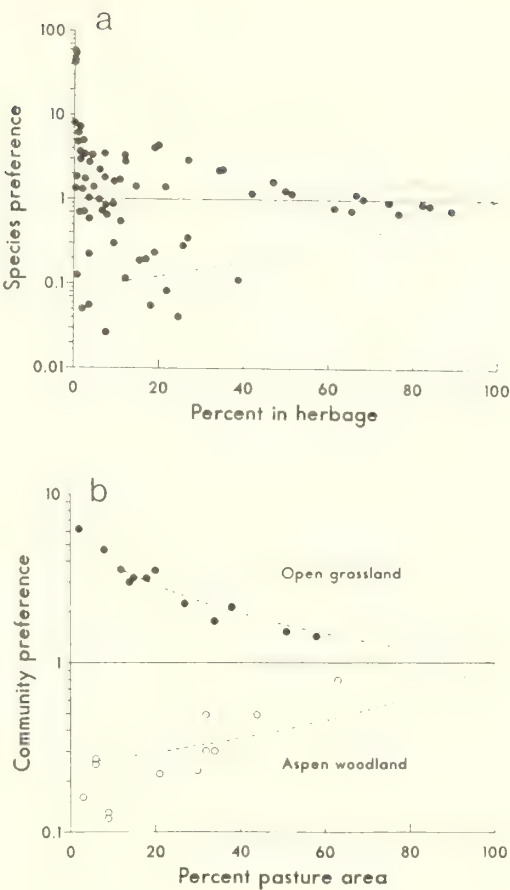


Figure 2.-- a. Effect of species relative abundance on dietary preferences. Dotted lines indicate predictions by the exponential species preference function for low- and high-quality plant species. Points indicate preferences observed on shortgrass steppe communities (Senft and others 1984). b. Effect of proportional mix of plant communities in a landscape mosaic on community preference (Senft 1986).

Table 1.-- Summary of domestic herbivore interactions with landscape pattern

Level of ecological organization	Units of selection	Foraging behavior	Aggregate response pattern	Environmental influences
Plant community	Plant species Individual plants Plant parts	Diet selection	Overmatching	Nutritive quality Plant architecture Secondary compounds
Landscape	Communities	Selection of feeding areas	Matching	Forage biomass and quality

are both animal species- and vegetation type-dependent, generalized models may be useful for predicting animal response to changes in plant community composition or to landscape mosaics of differing composition. Predictions of the foraging model may be useful in interpretation of field and laboratory studies of herbivore interactions with plants bearing anti-herbivore chemistry.

REFERENCES

- Allen, T. F. H.; Starr, T. B. Hierarchy: perspectives for ecological complexity. Chicago: University of Chicago Press; 1982. 310 p.
- Belovsky, G. E. Herbivore optimal foraging: a comparative test of three models. *Am. Nat.* 124: 97-115; 1984.
- Culley, M. J. Grazing habits of range cattle. *J. For.* 36: 715-717; 1938.
- Forman, R. T. T.; Godron, M. Patches and structural components for a landscape ecology. *BioScience*. 31: 733-740; 1981.
- Hanley, T. A. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. *J. Appl. Ecol.* 21: 423-436; 1984.
- Heady, H. F. Palatability of herbage and animal preference. *J. Range Manage.* 17: 76-82; 1964.
- Herrnstein, R. J. On the law of the effect. *J. Exp. Anal. Behav.* 13: 243-266; 1970.
- Hunter, R. F. Hill sheep and their pasture: a study of sheep-grazing in south-east Scotland. *J. Ecol.* 50: 651-680; 1962.
- Hunter, R. F. Home range behaviour in hill sheep. In: D. J. Crisp, ed., *Grazing in terrestrial and marine environments*. Oxford: Blackwell Scientific Publishers; 1964: 155-171.
- Moorefield, J. G.; Hopkins, H. H. Grazing habits of cattle in a mixed prairie pasture. *J. Range Manage.* 4: 151-157; 1951.
- Peterson, R. A.; Woolfolk, E. J. Behavior of Hereford cows and calves on shortgrass range. *J. Range Manage.* 8: 51-57; 1955.
- Provenza, F. D.; Malechek, J. C. Diet selection by domestic goats in relation to blackbrush twig chemistry. *J. Appl. Ecol.* 21: 831-841; 1984.
- Senft, R. L. Modeling dietary preferences of range cattle. *Proc. West. Sec. Am. Soc. Anim. Sci.* 35: 192-195; 1984.
- Senft, R. L. Cattle spatial use of mountain range: effects of grazing systems and landscape pattern. *Proc. West. Sec. Am. Soc. Anim. Sci.* 37: (in press); 1986.
- Senft, R. L.; Bowns, J. E.; Bagley, C. F. Shifts in cattle and sheep diets under various grazing systems on mountain pastures. *Proc. West. Sec. Am. Soc. Anim. Sci.* 37: (in press); 1986.
- Senft, R. L.; Rittenhouse, L. R.; Woodmansee, R. G. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. *J. Range Manage.* 38: 82-87; 1985.
- Senft, R. L.; Stillwell, M. A.; Rittenhouse, L. R. Diets selected by cattle from plant communities on shortgrass range. *Proc. West. Sec. Am. Soc. Anim. Sci.* 35: 180-183; 1984.

SNOWBERRY (SYMPHORICARPOS OREOPHILUS) DEFOLIATION BY SHEEP:

AN EXAMPLE OF SELECTIVE BROWSING

Calvin F. Bagley, G. B. Ruyle, and James E. Bowns

ABSTRACT: Diet selection decisions made by herbivores include selection among plant species, individual plants, and plant parts. This paper describes how the shrub snowberry was selectively defoliated by sheep. Leaf-to-stem ratios were sampled using an inclined-point frame, before and after sheep browsing. Additionally, browsed snowberry stems were counted in randomly located plots and browsing method (leaves stripped from the stem or entire stems removed) was recorded. Sheep usually stripped the leaves from the stem, rarely removing any part of stem, significantly reducing leaf-to-stem ratios. Because leaves were selectively removed the traditional concept of utilization as percent removal of current year's growth may not be applicable for determining sheep grazing pressure on snowberry and similar browse species.

INTRODUCTION

Snowberry (Symphoricarpos oreophilus Gray) provides a valuable source of forage for sheep on southwestern Utah summer ranges, even when herbaceous vegetation is not limiting (Bowns 1971; Bowns and Matthews 1983; Ruyle and Bowns 1985). To determine desirable stocking rates on rangelands, accurate methods of estimating utilization of snowberry and other shrubs by livestock and wildlife are important. Many methodologies for estimating shrub utilization have been developed (Bowns 1978) but, due to the mechanics of browsing behavior in sheep and other herbivores, interpretation of the estimates from some standard sampling techniques is difficult unless these techniques are altered or qualified in some way. When browsing, sheep generally strip the leaves from the stem, leaving the stem intact. The percentage of measured biomass removed compared to total year's growth is therefore relatively low. This selective harvesting of leaves results in most of the plant's photosynthetic material being removed, and causes greater stress on the plant than would be interpreted by estimates of biomass removed.

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Recent emphasis has been placed on a method of correlating browsed twig-diameter relationships to utilization (Basile and Hutchings 1966; Jensen and Urness 1981; Provenza and Urness 1981). Regression equations have been developed using this technique for snowberry on mountain pastures in southwestern Utah by Ruyle and others (1983). The inclined-point frame is another useful sampling tool that can be used for a nondestructive assessment of a shrub's vegetative structure. The point frame is used to measure the relative frequency of foliage area and a ratio of various plant parts to one another (such as, leaf:stem, green:dead; Warren-Wilson 1960, 1963, 1967). An automated point frame system can minimize errors; the fixed nature of the point diameter, which never exceeds 25 μ m, reduces subjectivity of the operator and increases sampling speed (Caldwell and others 1983).

Our study examined the selective browsing behavior of sheep. Our purpose was to use leaf-to-stem ratios to quantify the observed selective browsing of leaves, and to compare this measurement of selective defoliation with the regression model of twig-diameter relationships and the percentage of grazed stems.

STUDY AREA

The experiment was conducted on a mountain rangeland in southwestern Utah near Cedar City. The study area was located on a high mountain loam range site at an elevation of 2 500 m. Vegetation consisted of a mosaic of aspen (Populus tremuloides) with a snowberry understory interspersed with open areas of grassland and snowberry. Kentucky bluegrass (Poa pratensis) and Letterman needlegrass (Stipa lettermanii) were important associated grasses.

METHODS

An automated fiber-optic point frame (fig. 1; Caldwell and others 1983) with a 32.5° inclination (Warren-Wilson 1960) was used to compare changes in leaf:stem ratios resulting from grazing by sheep. The fiber-optic probe optically recognizes vegetation contacts, termed hits, as it penetrates the shrub canopy. When a plant part is detected the motorized probe stops and a record of the part hit is made. One location with 70 pin travels through the canopy was sampled in 1982 and three locations

(replications) with 50 pin travels each, were sampled in 1983. Due to the evenness of use in the small paddock and the small variation found in the first year's sample, three locations were determined to be an adequate sample size. For each pin travel a record of each hit on a snowberry leaf or a current year's stem was recorded, before and after sheep browsed the paddock (Ruyle 1983). Leaf:stem ratios were estimated by:

$$\text{Leaf:stem} = \text{Leaf hits} : \text{Stem hits} \quad (1)$$

In both, years snowberry utilization was estimated using a method developed by Ruyle and others (1983) in which caliper measurements of the last intact internode on browsed stems were used to predict biomass removed by browsing. Two models were used to predict the amount of biomass removed. These models distinguished between two kinds of browsing--leaf only and entire stem removal. Utilization derived from this regression technique is defined as:

$$\text{Percent biomass removed} = \frac{\text{Biomass removed}}{\text{Biomass produced}} \times 100 \quad (2)$$

In addition to this regression procedure grazed and ungrazed stems were counted and the percentage of grazed stems calculated. Percent grazed stems is defined here as:

$$\text{Percent grazed stems} = \frac{\text{Total stems grazed}}{\text{Total stems}} \times 100 \quad (3)$$

During 1982, 20 ewes with lambs were confined to a 0.4-ha (1-acre) paddock for 5 days. In 1983, 11 ewes with lambs were confined in the same 0.4-ha paddock for 9 days. The resulting stocking rates were 0.60 ha/AUM (animal unit month) in 1982 and 0.61 ha/AUM in 1983, where 1 AUM is the equivalent of five ewes and lambs grazing for 1 month.

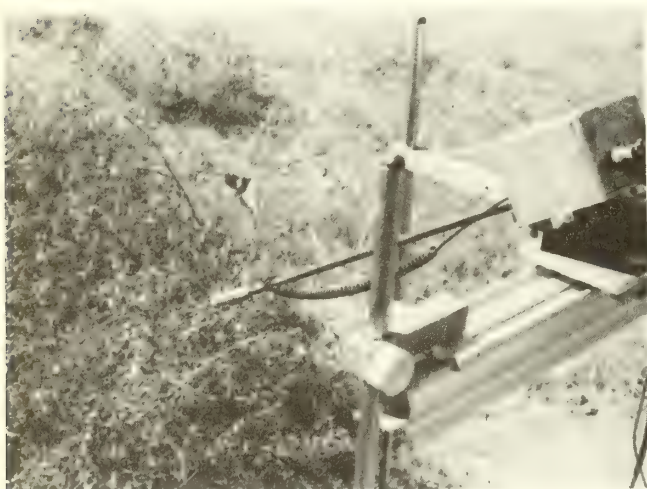


Figure 1.--Automated fiber-optic point frame system, in position to sample mountain snowberry.

RESULTS AND DISCUSSION

A comparison of the two utilization estimation methods showed a large disparity (fig. 2). The regression technique estimated biomass removed to be 33 percent, which indicates a low to moderate level of use. The grazed stems method estimated utilization to be 87 percent, indicating a heavy level of use. The selective browsing behavior of

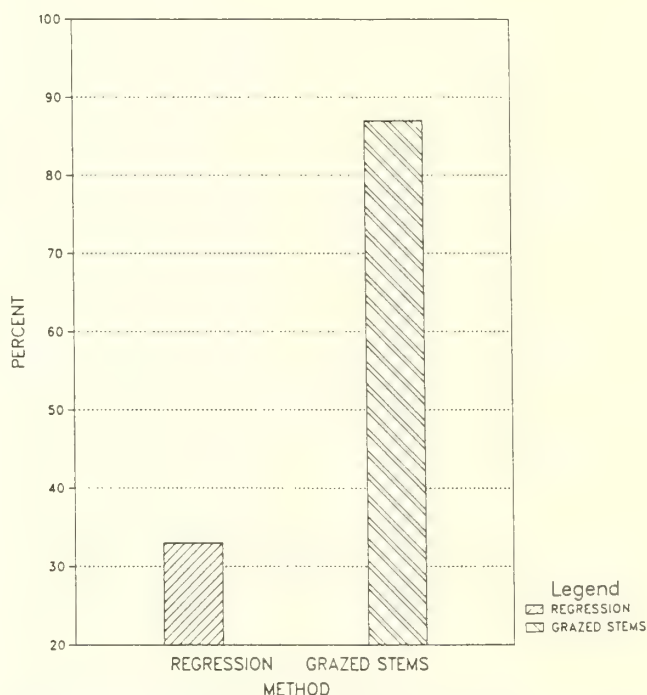


Figure 2.--Comparisons of two utilization estimation techniques. Twig-diameter regression estimate of percentage of biomass removed compared with the percentage of all stems that were grazed.

sheep provides an explanation for this disparity. When sheep browse snowberry they generally strip leaves from the stem leaving the stem intact (Ruyle and Bowns 1985) resulting in a high percentage of grazed stems but only a small amount of the plant biomass removed. In other research Ruyle and Bowns (1985) suggest that the upper limit of snowberry use by sheep, as estimated by the regression technique, is about 45 percent. A stand of snowberry that has been grazed at this intensity for several years is currently in low vigor with little or no regeneration.

Leaf:stem ratios for pre- and postbrowsing were calculated using the point frame method and are shown in table 1. Leaf:stem ratios before browsing were 3.59 leaves per green stem and 0.34 leaves per green stem after browsing in 1982. The same paddock was grazed at similar stocking rates in 1983. The experiment yielded nearly identical results, leaf:stem ratios were 3.58 before browsing and 0.41 after browsing ($p < 0.01$).

Table 1.--Leaf:stem ratios before and after browsing by sheep

	Year	
	1982	1983
Before browsing	3.58	13.59 ^a
After browsing	0.34	0.41 ^b

¹Means within columns followed by a different letter are significantly different P < 0.01.

In addition to the leaf:stem ratios obtained from the point frame data, we have calculated the percentage of leaves removed:

$$\text{Percent leaves removed} = \frac{\text{Leaves removed}}{\text{Total leaves}} \times 100 \quad (4)$$

This helps describe the impact on the shrub, in terms of the amount of photosynthesizing material (leaves) harvested after a browsing event. These data are compared (fig. 3) with the percent grazed stems and the percent biomass removed. At this moderate level of biomass removed (33 percent), 87 percent of the stems were grazed and over 85 percent of the leaves were removed. The few leaves that remained on the shrub were deep within the canopy.

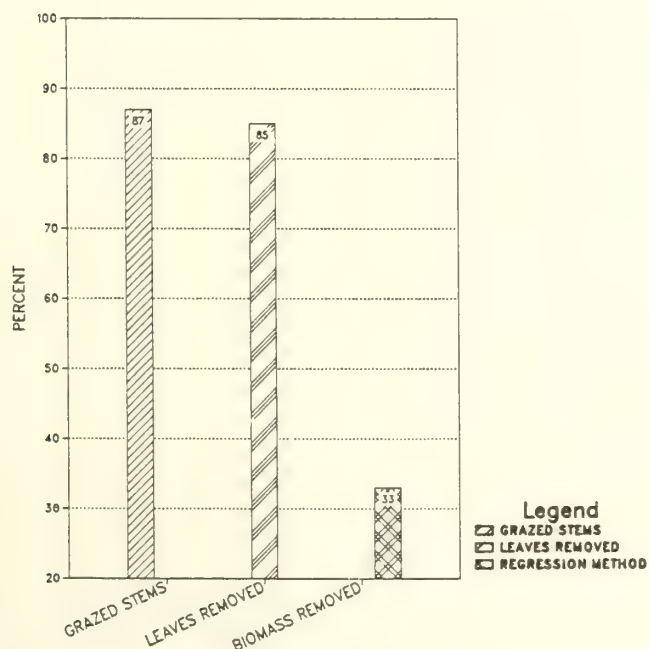


Figure 3.--Comparisons of three utilization estimation techniques. Percentage of grazed stems, percentage of leaves removed, and percentage of biomass removed.

CONCLUSIONS

Changes in leaf-to-stem ratios were compared with two utilization estimation techniques to provide insight into selective leaf removal by sheep. The true impact of this browsing behavior on the shrub is best described by the point frame data. Significant reductions in leaf:stem ratios occurred indicating high levels of photosynthetic material lost at low estimates of biomass removed as determined by traditional methods. When utilization was estimated to be 45 percent by the regression technique, the percentage of grazed stems ranged from 80 to 97 percent. Grazed-stem estimates are highly variable at levels greater than 80 percent. They have a poor correlation ($r^2 < 60$ percent; Bowns unpublished data) with biomass-removed estimates and present a greater risk for potential estimation error (Stickney 1966). Twig-diameter regression models, which account for both stems that are stripped of leaves and stems that are bitten off, provide accurate estimates of biomass removed and are a valuable sampling technique.

Careful interpretation of estimated values of biomass removed is important when selective browsing as described here is observed. Most recommended proper use levels of 50 to 60 percent or greater (Stoddart and others 1975) are based on winter use of deciduous browse species. Evaluation of the defoliation patterns is important in accurately assessing the degree of utilization of a valuable forage source such as snowberry, and other broad-leaved shrubs such as serviceberry (*Amelanchier alnifolia*), mountain mahogany (*Cercocarpus* spp.), and aspen where summer leaf stripping routinely occurs. Proper utilization levels for shrubs browsed in the summer need to be adjusted downward from recommended winter use levels when management goals require maintaining snowberry or other shrubs in good vigor and abundance.

REFERENCES

- Basile, J. V.; Hutchings, S. S. Twig diameter-length-weight relations of bitterbrush. *J. Range Manage.* 19: 34-38; 1966.
- Bowns, James E. Sheep behavior under unherded conditions on mountain summer ranges. *J. Range Manage.* 24: 105-109. 1971.
- Bowns, James E. Methodologies for determining cover, production, and utilization of woody sagebrush species. In: *The sagebrush ecosystem: a symposium: proceedings*; 1978 April; Logan, UT:Utah State University; 1978: 220-229.
- Bowns, James E. Unpublished data on file. Southern Utah State College, Cedar City, Utah. 1983.
- Bowns, James E.; Matthews, D. H. Cattle grazing with sheep--a plus for rangelands and production. *Utah Science.* 44(2): 38-43; 1983.

- Caldwell, M. M.; Harris, G. W.; Dzurec, R. S. A fiber optic point quadrat system for improved accuracy in vegetation sampling. *Oecologia*. 59: 417-418; 1983.
- Jensen, C. H.; Urness, P. J. Establishing browse utilization from twig diameters. *J. Range Manage.* 34: 113-116; 1981.
- Provenza, F. D.; Urness, P. J. Diameter-length-weight relations for blackbrush (*Coleogyne ramosissima*) branches. *J. Range Manage.* 34: 215-217; 1981.
- Ruyle, G. B. Sheep diets and feeding behavior in single and common use grazing trials on southwestern Utah summer range. Logan, UT: Utah State University; 1983. 124 p. Dissertation.
- Ruyle, G. B.; Bowns, James E. Forage use by cattle and sheep grazing separately and together on summer range in southwestern Utah. *J. Range Manage.* 38: 299-302; 1985.
- Ruyle, G. B.; Bowns, James E.; Schlundt, Al F. Estimating snowberry (*Symphoricarpos oreophilus*) utilization by sheep from twig diameter-weight relations. *J. Range Manage.* 36: 472-774; 1983.
- Stickney, Peter F. Browse utilization based on percentage of twig numbers browsed. *J. Wildlife Manage.* 30: 204-206; 1966.
- Stoddart, L. A.; Smith, A. D.; Box, T. W. Range management. 3d ed. New York: McGraw-Hill; 1975. 532 p.
- Warren-Wilson, J. Inclined point quadrats. *New Phytol.* 59: 1-8; 1960.
- Warren-Wilson, J. Estimation of foliage denseness and foliage angle by inclined point quadrats. *Aust. J. Bot.* 13: 95-105; 1963.
- Warren-Wilson, J. Stand structure and light penetration. III. Sunlit foliage area. *J. Appl. Ecol.* 4: 159-165; 1967.

Section 5. Plant Response to Browsing

GROWTH, NUTRIENT, AND WATER STATUS OF JOJOBA (SIMMONDSIA CHINENSIS)

IN RELATION TO LIVESTOCK GRAZING

Bruce A. Roundy, George B. Ruyle, Albert K. Dobrenz
Van Wilson, and Don Floyd

ABSTRACT: Jojoba is a nutritious shrub of major seasonal forage value in its midelevational range in the Sonoran Desert. Its ability to regrow and maintain similar ratios of photosynthetic to non-photosynthetic biomass, and similar water status when heavily grazed or ungrazed indicates high tolerance to grazing. Moderate grazing is recommended to maintain shrub size and forage production.

INTRODUCTION

Jojoba (Simmondsia chinensis) is a drought-tolerant, long-lived evergreen shrub of the Sonoran Desert in the southwestern United States and northwestern Mexico. It is distributed over about 26 million ha predominantly on desert foothills and washes between 600 and 1 200 m elevation (Gentry 1958). Jojoba nuts contain wax esters suited to a variety of commercial uses, especially as substitutes for sperm whale oil in the manufacture of high pressure lubricants (Scarlett 1978). Extensive research continues to be directed at potential uses and domestication of jojoba (Elias-Cesnik 1982). Jojoba is also an important component of the desert ecosystem, furnishing food for rodents (Sherbrooke 1976), birds (Thomson 1976), javelina (Pecari tajaco) (Knipe 1956), desert bighorn sheep (Ovis canadensis) (Russo 1956), and mule deer (Odocoileus hemionus) (Judd 1962; Urness and others 1977), as well as forage for domestic livestock (Mills and Foster 1982). After the annual forbs and grasses senesce in early summer in central Arizona, jojoba may comprise up to 50 percent of the diet of cattle (Aguirre de Luna 1980).

The commercial and ecological value of jojoba has prompted concern over its use and management as a forage. The U.S. Department of Agriculture, Forest Service currently manages jojoba by limiting utilization to 40 percent of current year's growth under a continuous grazing system and 50 percent under a rest rotation grazing system (USDA Forest Service 1979). The effects of heavy herbage removal have not been quantified (Mills and Foster 1982) or

compared with the effects of moderate utilization that is currently recommended by the Forest Service.

Caldwell (1984) recently summarized the current knowledge of factors important to grazing tolerance. Of major importance is the availability of apical meristems and ability of lateral buds to initiate regrowth and replace grazed shoots. Pruning of jojoba stimulates vegetative growth (Yermanos 1980). Jojoba may withstand heavy browsing (Judd 1962), but seed and foliage production are reportedly greatly reduced (Mills and Foster 1982). Moderately grazed jojoba shrubs may be smaller than ungrazed plants (Ruyle and Roundy 1985) but may have more stems and leaf pairs per branch than lightly grazed shrubs (Roundy and others 1986). The above observations suggest that removal of the apical buds of jojoba by grazing or pruning may stimulate twig growth from lateral buds as occurs with many other shrubs (Garrison 1971). Livestock producers have suggested that grazing of jojoba results in greater current year's growth than occurs on ungrazed plants and that new growth is more palatable and nutritious than old growth.

A major influence on persistence of plants that are grazed is the competitive environment of the associated plant community (Caldwell 1984). Defoliation of plants in semiarid and arid environments may limit their growth when soil water is available. Ungrazed plants may then use the available water and nutrients not used by grazed plants and expand their shoots or roots to preempt future resource use by grazed plants. Thus the ability of plants to maintain a favorable water balance and grow when grazed is essential for retention of competitive status in the community and is a good indication of tolerance to grazing.

The purposes of this study were to characterize the nutritional quality of jojoba and to quantify its growth and water status in relation to different grazing intensities.

Specific objectives included:

1. Compare seasonal crude protein and phosphorous levels of previous and current year's growth.
2. Compare twig initiation and growth and photosynthetic biomass percentages of ungrazed, moderately grazed, and heavily grazed shrubs.
3. Compare water stress, transpiration, stomatal resistance, and leaf temperature of ungrazed, moderately grazed, and heavily grazed plants.

Paper presented at the Symposium on Plant-Herbivore Interactions, Snowbird, UT, August 7-9, 1985.

Bruce A. Roundy is Assistant Professor of Range Management, George B. Ruyle is Range Management Specialist, Albert K. Dobrenz is Professor of Plant Sciences, Van Wilson is Agriculture Extension Agent, and Don Floyd is Assistant Extension Specialist, all at the University of Arizona, Tucson.

STUDY AREA AND METHODS

The study area is on a fan piedmont (Peterson 1981) south of Roosevelt Lake in southern Arizona. It is a clayloam upland range site supporting Upper Sonoran Desert shrub vegetation including paloverde (*Cercidium microphyllum*), wolfberry (*Lycium exsertum*), mesquite (*Prosopis juliflora*), various species of cholla and prickly pear (*Opuntia*) in addition to jojoba. Herbaceous vegetation is mainly restricted to annuals (*Bromus rubens* and *Erodium cicutarium*) and a few remnant perennial three-awns (*Aristida* spp). On the site is a 49-year-old enclosure and, nearby, a stock water pond at least as old as the enclosure. Cattle have continuously grazed the area outside the enclosure since it was built. In close proximity and on the same aspect are ungrazed jojoba plants in the enclosure, plants that are heavily grazed near the pond, and plants that are moderately grazed about 0.5 km from the pond. To determine seasonal nutritional quality, we collected samples of current and previous year's growth from four shrubs monthly from July 1978 to June 1979. Also in June 1985 samples of current and previous year's growth were collected from 20 shrubs. Samples were oven dried and ground thoroughly with a Wiley mill equipped with a 40-mesh screen. Total nitrogen was determined by the macro-Kjeldahl method (Bremner 1965). Phosphorus was analyzed following the procedure described by Chapman and Pratt (1961).

Growth patterns were determined by diagramming three branches on each of 10 ungrazed, moderately grazed, and heavily grazed shrubs. Branches were first diagrammed on March 5, 1985 and rediagrammed May 15, 1985. This was the period of expected maximum growth. Current year's (green) growth, old nongreen stems, leaf pairs, and grazed stems were diagrammed and all internodes were measured. Twig lengths removed by grazing were estimated from measurements of stem diameter at the point of grazing using a linear regression of twig length on stem diameter calculated from 100 observations from shrubs on the study site. To determine percentages of photosynthetic biomass within the canopy, we collected two entire main branches from each of 10 ungrazed, moderately grazed, and heavily grazed plants. Branches were collected the end of June to be representative of spring growth. Branches were clipped at 5-cm increments perpendicular to the main stem. Old leaves, current year's leaves, green stems, and brown stems were separated, oven dried, and weighed.

Plant water status was quantified by measuring transpiration, stomatal resistance, and leaf temperatures with a LICOR LI-1600 steady-state porometer and by measuring xylem water potential with a pressure bomb (Sholander and others 1965) after enclosing twigs in a plastic bag (Wenkert and others 1978). Measurements were taken on four to five shrubs each that were ungrazed, moderately grazed, or heavily grazed. Measurements were taken from predawn through the day on May 15 and on July 2. In addition, carbon uptake was sampled on new and old leaves for 15 to 20 shrubs on April 12 and May 22. Measurements were taken between 10 a.m. and 1 p.m. A branch portion was enclosed

in a 0.1411-L cuvette for 60 seconds and the difference in CO_2 concentration was measured from air samples taken with syringes and later injected into an infrared CO_2 analyzer (Clegg and others 1978). Measurements of CO_2 taken in this manner estimate net photosynthesis or gross photosynthesis minus light and dark respiration. Leaf areas were measured with a LICOR LI-3100 area meter.

Treatments were tested for significance ($p < 0.05$) using analysis of variance with shrubs as sample units and, where appropriate, branches as subsamples. When treatments were significant, means were compared using Duncan's multiple range test.

RESULTS AND DISCUSSION

Forage Quality

Jojoba forage is high in crude protein and phosphorus during the spring (fig. 1). New growth had higher nutritive quality than old plant material, except December through March. Leaves and stems produced in the spring of 1985 were significantly higher in both crude protein (11.7 percent) and phosphorus (0.15 percent) than previous year's growth (6.7 percent and 0.07 percent, respectively), but both were adequate to satisfy dietary requirements of cows for these nutrients if intake is

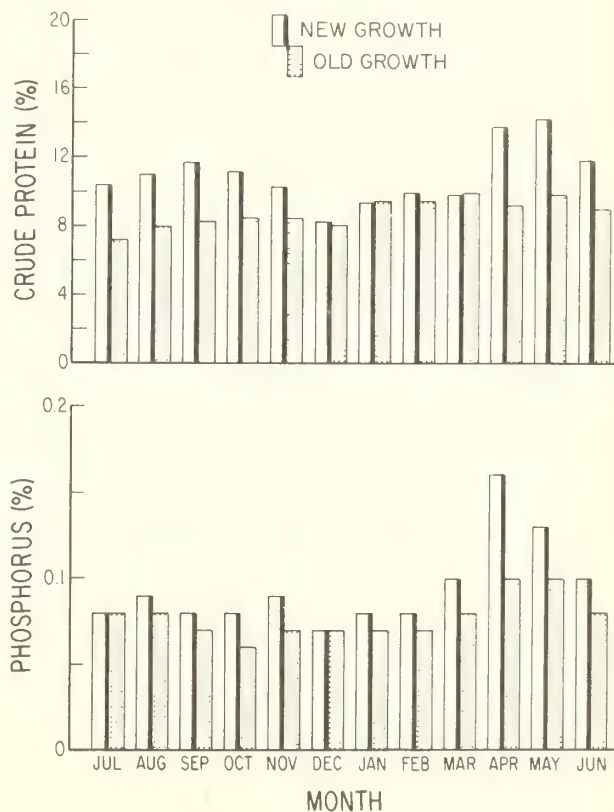


Figure 1.--Crude protein and phosphorus percentages of current and previous year's growth of jojoba shrubs sampled near Roosevelt Lake, AZ in 1978 and 1979.

normal. Jojoba clearly offers nutritive forage year round for livestock and wildlife.

Twig Initiation and Growth

Jojoba produces opposite leaves; new shoots initiate from lateral buds in the leaf axils or from apical meristems. Actively growing twigs produced this year had green stems. Percentage grazed twigs of total twigs by mid-May was 0, 38, and 63 percent for diagramed branches on ungrazed, moderately grazed, and heavily grazed shrubs, respectively. The number of new twigs initiated per centimeter of total nongreen twig length was statistically similar for all grazing treatments (table 1). Ungrazed branches had more apical buds per centimeter of nongreen twig length than grazed branches, but both grazed and ungrazed branches had similar numbers of new twigs produced per apical bud. All branches had similar numbers of lateral bud pairs per centimeter of total nongreen twig length, but grazed branches had significantly more new twigs initiated per lateral bud pair than ungrazed branches. Grazing removes apical buds, thereby stimulating new twig growth from lateral buds. New twig initiation from lateral buds compensates for loss of twigs that could have been produced from apical buds but does not necessarily result in greater total new twig initiation on grazed than ungrazed plants.

Table 1.--New twigs, buds, and twig growth of jojoba shrubs in relation to cattle grazing intensity south of Roosevelt Lake, AZ

Parameter	Grazing intensity		
	Ungrazed	Moderately grazed	Heavily grazed
New twigs per cm of nongreen twig length (No.)	¹ 0.35a	0.35a	0.49a
Apical buds per cm of nongreen twig length (No.)	0.15a	0.05b	0.06b
New twigs per apical bud (No.)	1.25a	1.69a	1.78a
Lateral bud pairs per cm of nongreen twig length (No.)	0.38a	0.34a	0.40a
New twigs per lateral bud pair (No.)	0.41b	0.80a	1.10a
New twig length May 15, 1985 (cm)	2.9a	3.2a	3.5a
New twig growth March 5 to May 15, 1985 (cm)	2.2a	2.9a	3.3a

¹Means in rows followed by the same letter are not significantly different ($P < 0.05$) by Duncan's multiple range test.

The period of greatest twig growth was between March and mid-May. Mean length of current year's twigs was statistically similar for all grazing treatments on May 15. Mean twig growth between March 5 and May 15 was also similar for all treatments (table 1). In this study, grazing did not result in either increased or decreased growth of jojoba twigs.

Spring growth of twigs in this study was much greater than that reported by Guedes Almeida (1979) and Paes De Oliveira (1983). In the present study, leader growth is reported as the average length of twigs that actually elongated. Elongation occurred on about 60 percent of the more than 2,000 twigs that were measured. Measurement of fewer marked twigs, some of which may not elongate, may not be representative of active leader growth on jojoba and other woody plants (Paes De Oliveira 1983). Diagraming branches with numerous twigs is a very tedious, but more thorough, approach to quantifying woody plant growth.

Photosynthetic Biomass

Ungrazed shrubs had a higher percentage photosynthetic biomass of total biomass down through the shrub canopy than grazed shrubs (fig. 2). Total photosynthetic biomass per branch was similar for ungrazed and moderately grazed plants to a depth of 40 cm into the canopy, and to this depth was much higher for ungrazed and moderately grazed than heavily grazed plants. Grazed plants and ungrazed plants had statistically similar nonphotosynthetic biomass through the canopy but ungrazed plants had a much larger woody main stem below the canopy than grazed plants. Ungrazed and moderately grazed plants had similar total photosynthetic biomass per main branch; that for heavily grazed plants was much lower (table 2). However, due to their larger woody stems below the canopy, ungrazed plants had much greater total nonphotosynthetic biomass per branch and therefore a similar percentage photosynthetic of total biomass per branch as grazed plants. Heavily grazed and ungrazed shrubs had equal ratios of photosynthetic to nonphotosynthetic biomass, but branches of heavily grazed shrubs are much smaller, so they produce much less green forage per branch than ungrazed or moderately grazed shrubs.

Heavy grazing reduced shrub size. Heights of ungrazed, moderately grazed, and heavily grazed shrubs averaged 145, 82, and 56 cm, respectively. Numbers of main branches per shrub averaged 39, 50, and 31, respectively, for ungrazed, moderately grazed, and heavily grazed shrubs. Multiplying out averages of green weight per branch, number of branches per shrub, and number of shrubs per hectare gave estimates of green forage yields of 3 382, 3 163, and 516 kg·ha⁻¹ for ungrazed, moderately grazed, and heavily grazed shrubs, respectively. Although jojoba may maintain growth and sufficient photosynthetic biomass in a dense canopy to survive under heavy grazing, shrub size and forage production per shrub are greatly reduced. In contrast, moderate utilization results in almost as much green forage as that produced by ungrazed plants.

Grazed plants had a higher percentage new leaf of total photosynthetic biomass than ungrazed plants (table 2). Ungrazed plants tended to have a greater percentage old leaf of total photosynthetic biomass than grazed plants. Stem biomass was less than one-third of the total biomass, and grazed and ungrazed plants had similar stem biomass percentages.

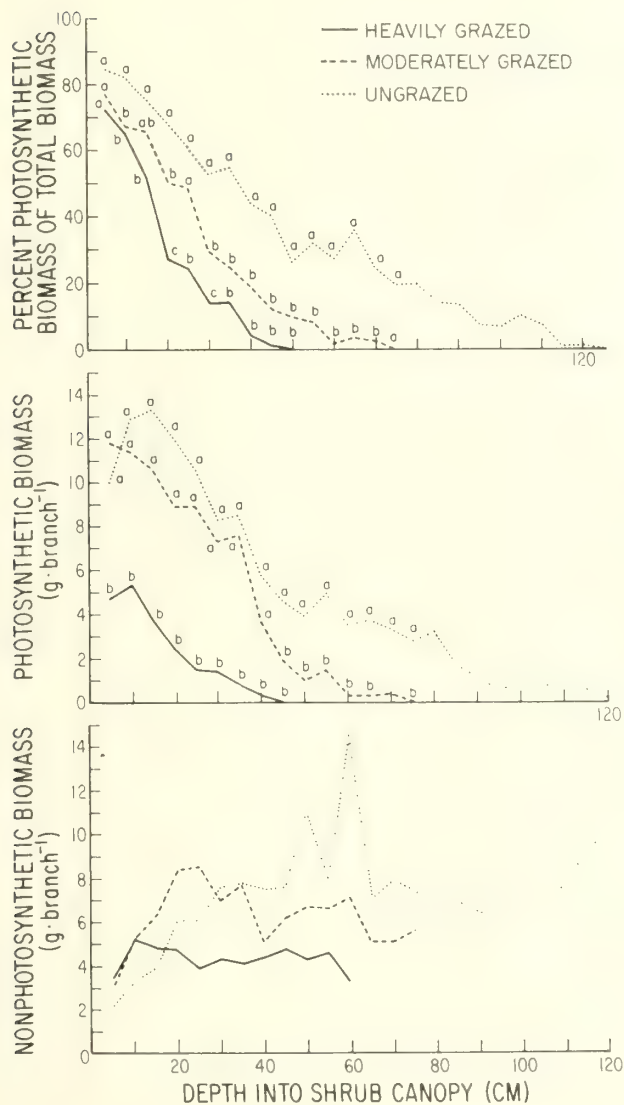


Figure 2.--Percent photosynthetic biomass of total biomass (top), photosynthetic biomass (middle), and nonphotosynthetic biomass (bottom) of jojoba shrubs in relation to intensity of livestock grazing near Roosevelt Lake, AZ. Points at the same depth with the same letter are not significantly different ($P < 0.05$) by Duncan's multiple range test. No significant differences occurred for nonphotosynthetic biomass.

Table 2.--Photosynthetic and nonphotosynthetic biomass and percentages for main branches of jojoba in relation to grazing intensity

Parameter	Grazing intensity		
	Ungrazed	Moderately grazed	Heavily grazed
Photosynthetic biomass per branch (g)	116.7a	75.9a	20.3b
Nonphotosynthetic biomass per branch (g)	168.1a	85.5b	36.3b
Percent photosynthetic of total branch biomass	44.1a	46.6a	40.8a
Percent new leaf of total photosynthetic biomass	33.9b	47.6a	49.2a
Percent old leaf of total photosynthetic biomass	38.5a	28.0a	30.4a
Percent stem of total photosynthetic biomass	27.6a	24.4a	20.4a

¹ Means in rows followed by the same letter are not significantly different ($P < 0.05$) by Duncan's multiple range test.

Photosynthetic Rates

Newly developed leaves generally had higher net photosynthetic rates than previous year's leaves especially when carbon uptake was expressed per dry weight of leaves (table 3). New leaves had a much lower specific leaf weight than previous years' leaves, and their specific leaf weight increased with age. Photosynthetic rates apparently decreased with foliage age and were low compared to those reported at similar values of plant water stress in the literature. Midday plant water stress averaged about 3.5 to 4.0 MPa on May 15 in this study (fig. 3). Net photosynthetic rates reported at these values of water stress included less than 1 to 6 $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$ (Glat and others 1983), 6 to 13 $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$ (Adams and others 1977), and less than 1 to 9 $\text{mg CO}_2 \cdot \text{g}^{-1} \text{ dry wt} \cdot \text{h}^{-1}$ (Al-Ani and others 1972). Although jojoba has low photosynthetic rates compared to many plants (Rawson and others 1977), it can photosynthesize at very low water potentials. Photosynthetic rates may vary substantially among different clones (Glat and others 1983).

Water Status

Above-normal precipitation fell in the winter of 1984-85, but little or no precipitation occurred in May through early July when plant water status was measured (fig. 4). Vapor pressure deficits and leaf temperatures were high and increased through the day (fig. 3). Leaf temperatures were usually slightly higher but within 1 °C of air temperature.

15 MAY 1985

2 JULY 1985

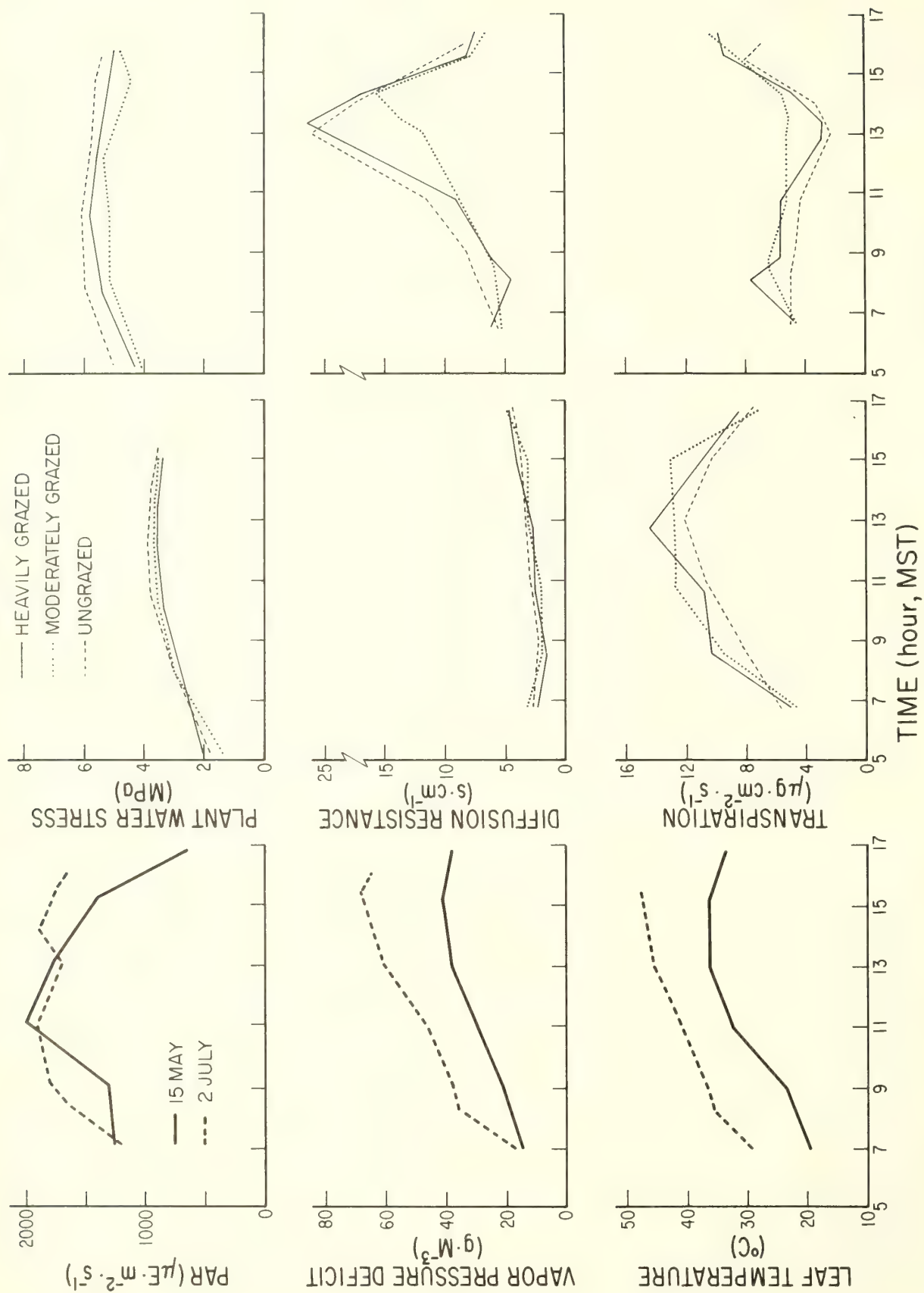


Figure 3.--Incident photosynthetically active radiation (PAR), vapor pressure deficit, leaf temperature, plant water stress, diffusion resistance, and transpiration for jojoba shrubs near Roosevelt Lake, AZ.

Table 3.--Net photosynthesis and specific leaf weights for old and new jojoba leaves sampled near Roosevelt Lake, AZ

Leaves	Net photosynthesis				Specific leaf weight	
	$(\text{mgCO}_2 \cdot \text{dm}^{-2} \text{ leaf area} \cdot \text{h}^{-1})$		$(\text{mgCO}_2 \cdot \text{g}^{-1} \text{ dry wt} \cdot \text{h}^{-1})$		$(\text{g} \cdot \text{dm}^{-2})$	
	12 April	22 May	12 April	22 May	12 April	22 May
Old	¹ 1.75a	0.80c	0.49c	0.26d	3.72a	3.23a
New	1.97a	1.18b	1.72a	0.67b	1.26c	1.75b

¹Means in the same units followed by the same letter have overlapping 95 percent confidence levels.

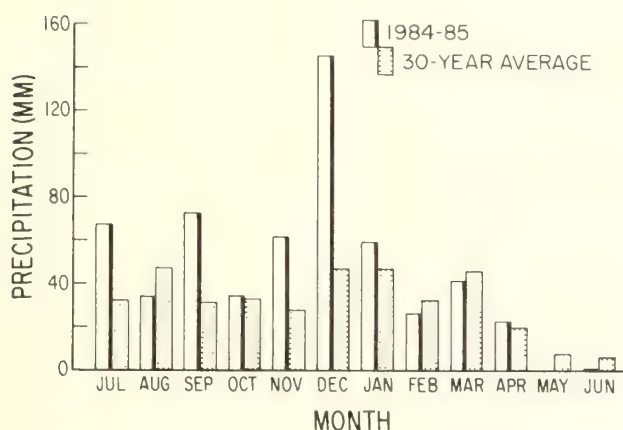


Figure 4.--Monthly precipitation at Roosevelt Lake, AZ.

In May, predawn plant water stress averaged 1.9 MPa and increased to an average maximum of 3.6 MPa at midday. Transpiration rates increased with increasing leaf temperatures and vapor pressure deficits and then decreased in the afternoon. Diffusion resistance was low and increased only slightly through the day even though plant water stress increased 1.7 MPa. By July vapor pressure deficit, leaf temperature, and plant water stress all increased markedly. Transpiration rates were low compared to May and dropped to a minimum at midday as diffusion resistance increased rapidly. Transpiration then increased as diffusion resistance decreased even though plant water stress remained high. This pattern of diffusion resistance indicates a temporary period of stomatal closure at midday.

Leaf temperatures, plant water stress, transpiration, and diffusion resistance were similar for the three grazing treatments on both sample dates (fig. 3). Only at midday on July 2 were there statistically significant differences; moderately grazed plants had higher transpiration and lower diffusion resistance than ungrazed plants. Ungrazed plants showed a trend toward slightly greater water stress than grazed plants, but differences were not statistically significant.

Indications are that grazed and ungrazed plants were able to maintain a similar water balance, even during a period of high plant water stress. Regression estimates of leaf area from biomass measurements indicated that ungrazed and moderately grazed plants had similar leaf areas and about six times the leaf area of heavily grazed shrubs. Assuming transpiration rates per leaf area are similar, ungrazed and moderately grazed shrubs could potentially transpire six times more water than heavily grazed shrubs. Provided their root systems are extensive enough to satisfy this high transpirational demand, ungrazed and moderately grazed plants could be more competitive for soil water than heavily grazed shrubs. The similar water status of grazed and ungrazed shrubs indicated a similar ability to balance transpirational water loss with water uptake through the root system. Even though heavily grazed shrubs may have smaller root systems than the larger ungrazed and moderately grazed shrubs, their lower total leaf area and probable lower transpirational water loss could allow these shrubs to maintain a water balance similar to the larger shrubs, provided the soil water available to their roots is not exploited by other plants. This is a fairly open plant community. Foliar cover of jojoba averages 14 percent inside the enclosure and 7 percent outside. Cover of all other shrubs averages 22 percent. The clayey soil has a high water holding capacity. Heavily grazed and moderately grazed plants appear to be maintaining at least as favorable a water balance as ungrazed plants. Jojoba's high drought tolerance is well evidenced by continued transpiration and photosynthesis at what is considered extremely high plant water stress for most plants.

CONCLUSIONS

Jojoba is a nutritious forage for wildlife and livestock and is of major seasonal value. Jojoba is apparently very grazing tolerant, partly because it is able to initiate new twigs from lateral buds to compensate for loss of apical buds and twigs by grazing. Heavily grazed plants maintained as high a ratio of photosynthetic to total biomass as ungrazed plants. However, heavy grazing greatly reduced shrub size and forage yield. Moderate grazing resulted in forage yields similar to those

of ungrazed plants. Although grazing reduced shrub size, grazed plants maintained a water status similar to ungrazed plants, even during a period of high water stress in early summer. This indicates a comparable ability to balance transpirational water loss with water uptake through the roots. Although jojoba was tolerant of heavy grazing, moderate grazing is recommended to maintain greater shrub size and forage production.

REFERENCES

- Adams, J. A.; Johnson, H. B.; Bingham, F. T.; Yermanos, D. M. Gaseous exchange of *Simmondsia chinensis* (jojoba) measured with a double isotope porometer and related to water stress, salt stress and nitrogen deficiency. *Crop Science*. 17: 11-15; 1977.
- Aguirre de Luna, R. Cattle diets during spring and summer on desert shrub rangelands near Roosevelt Lake, Arizona. Tucson, AZ: University of Arizona; 1980. 68 p. Thesis.
- Al-Ani, H. A.; Strain, B. R.; Money, H. A. The physiological ecology of diverse populations of the desert shrub *Simmondsia chinensis*. *Journal of Ecology*. 60: 41-57; 1972.
- Bremner, J. M. Total nitrogen. In: Black, C. A.; Evans, D. D.; White, J. L.; Ensminger, L. E.; and Clark, F. E. eds. *Methods of soil analysis*, part 2. Agronomy 9. Madison, WI: American Society of Agronomy; 1965: 1172-1173.
- Caldwell, M. M. Plant requirements for prudent grazing. In: *Developing strategies for rangeland management*. National Research Council/National Academy of Sciences. Boulder, CO: Westview Press; 1984: 117-152.
- Chapman, H. D.; Pratt, P. F. *Methods of analysis for soils, plants and waters*. Riverside, CA: University of California, Division of Agricultural Sciences; 1961. 309 p.
- Clegg, M. D.; Sullivan, C. Y.; Eastin, J. D. A sensitive technique for the rapid measurement of carbon dioxide concentrations. *Plant Physiology*. 62: 924-926; 1978.
- Garrison, G. A. Carbohydrate reserves and response to use. In: McKell, C. M.; Blaisdell, J. P.; Goodin, J. R., eds. *Wildland shrubs - their biology and utilization*. General Technical Report INT-1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1971: 274-278.
- Gentry, H. S. The natural history of jojoba (*Simmondsia chinensis*) and its cultural aspects. *Economic Botany*. 12: 261-295; 1958.
- Glat, D.; Dobrenz, A. K.; Palzkill, D. A. Carbon dioxide exchange processes in jojoba (*Simmondsia chinensis*). *Desert Plants*. 5: 118-121; 1983.
- Guedes Almeida, F. A. Ecological studies of native jojoba plants--*Simmondsia chinensis* (Link) Schneider--in Arizona. Tucson, AZ: University of Arizona; 1979. 96 p. Dissertation.
- Elias-Cesnik, A. Jojoba guide to the literature. Tucson, AZ: University of Arizona, Office of Arid Land Studies; 1982. 221 p.
- Judd, B. I. Principal forage plants of southwestern ranges. Paper No. 69. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1962. 93 p.
- Knipe, T. The javelina in Arizona: a research and management study. *Wildlife Bulletin* 2. Phoenix, AZ: Arizona Game and Fish Department; 1956. 96 p.
- Mills, J. L.; Foster, K. E. Jojoba wild stands: natural history and use impacts. Final report for U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Tucson, AZ: University of Arizona, Office of Arid Land Studies; 1982. 71 p.
- Paes De Oliveira, J. Phenological studies of three natural stands of jojoba (*Simmondsia chinensis* (Link) Schneider) near Tucson, Arizona. Tucson, AZ: University of Arizona; 1983. 102 p. Dissertation.
- Peterson, F. F. Land forms of the Basin and Range province defined for soil survey. *Technical Bulletin* 28. Reno, NV: University of Nevada, Nevada Agricultural Experiment Station; 1981. 52 p.
- Rawson, H. M.; Begg, J. E.; Woodward, R. G. The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. *Planta*. 134: 5-10; 1977.
- Roundy, B. A.; Ruyle, G. B.; Ard, J. Estimating production and utilization of jojoba. In: *Symposium proceedings--Ecology, management, and economic value of arid land plants*. Saltillo, Mexico; Feb. 18-22: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report. (In press).
- Russo, J. P. The desert big horn sheep in Arizona: a research and management study. *Wildlife Bulletin* 1. Phoenix, AZ: Arizona Game and Fish Department; 1956. 153 p.
- Ruyle, G. B.; Roundy, B. The effect of long-term cattle grazing on jojoba (*Simmondsia chinensis*) in central Arizona. Society for Range Management 38th Annual meeting; Feb. 11-15. Salt Lake City, UT; Abstract 225; Society for Range Management, Denver, CO; 1985.

- Scarlett, P. L. Jojoba in a nutshell, Carpinteria, CA: Jojoba International Corporation; 1978. 55 p.
- Scholander, P. F.; Hammel, H. T., Bradstreet, F. D.; Hemmingsen, E. A. Sap pressure in vascular plants. Science. 148: 339-346; 1965.
- Sherbrooke, W. C. Differential acceptance of toxic jojoba seed (*Simmondsia chinensis*) by four Sonoran Desert heteromyid rodents. Ecology. 57: 596-602; 1976.
- Thomson, P. H., ed. California Rare Fruit Growers jojoba handbook. Special Publication 2. Bonsall, CA: California Rare Fruit Growers; 1976. 118 p.
- Urness, P. J.; Smith, A. D.; Watkins, R. K. Comparison of in vivo and in vitro dry matter digestibility of mule deer forages. J. Range Manage. 30: 119-121; 1977.
- U.S. Department of Agriculture, Forest Service. Allotment analysis handbook. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region; 1979.
- Wenkert, W.; Lemon, E. R.; Sinclair, T. R. Changes in water potential during pressure bomb measurement. Agronomy Journal. 70: 353-355; 1978.
- Yermanos, D. M. Review of seven years of performance data on jojoba under cultivation. Paper presented at fourth international conference on jojoba, Hermosillo, Sonora, Mexico; 1980. Nov. 5-8.

DIFFICULTIES IN INTERPRETATION OF LONG-TERM VEGETATION TRENDS

IN RESPONSE TO LIVESTOCK GRAZING

Warren P. Clary and Ralph C. Holmgren

ABSTRACT: Grazing effects data from the Desert Experimental Range, Utah, are used to illustrate the problems of interpreting vegetation response to grazing treatment, precipitation, and site. Differences in results and analysis may be related to experience, viewpoint, plot sampling, and failure to note climatic patterns, soils, and vegetation cycles.

INTRODUCTION

Hutchings (1966), summarizing 30 years of grazing effect observations in the shadscale zone of the Great Basin Desert of western Utah, stated that "response of vegetation varied widely, depending on weather, degree of depletion, and the quality of management applied." Desert plant communities are dynamic; their floristic composition may change, sometimes dramatically, over time (West 1982). Besides current weather and livestock, some of the factors acting and interacting to effect change are climatic cycles, other herbivores including invertebrates, and the inherent attributes of plant species such as their relative longevity, palatability, resistance to disease and defoliation, seeding habits, season of active growth, and adaptability to specific sites. With these and perhaps other factors operating, range managers, as Blaisdell and Holmgren (1984) have said, "may find it difficult to judge what part of any change is due to their actions or may be under their control."

That researchers have the same problem as managers in interpreting grazing effects is clear from the varying conclusions drawn from studies made with similar objectives. Conflicting claims are notorious, and different recommendations have come from studies of season and degree of herbage removal by clipping or grazing. Studies comparing grazing systems were reviewed and summarized by Hickey (no date), who found such a divergence of conclusions he warned that a land manager "restricted to a limited amount of literature . . . is more apt to be

misinformed than uninformed." Hickey suggested reasons for the differing results and conclusions; among them were: experience and viewpoint of the author, aspect of the problem stressed, duration of the study, confounding parameters, and improper or shaky extrapolation (especially from insufficiently measured aspects).

We even find disparity among separate reports from a single study that has been under way for half a century at the Desert Experimental Range (DER) in western Utah. These reports, discussed later, illustrate well the problems of interpreting data on vegetation response to grazing use. Although desert vegetation is floristically simple, and its response to applied treatments would seem straightforward, the reports from this single study provide evidence of the complexity of interpretation.

Only a part of the disparity found in the DER reports is related to a period of study or amount of data accumulated. Among the causes are some of those mentioned by Hickey. Other factors may be unique to this study. Our purpose here is threefold: to discuss briefly some previously published results and conclusions, adding information from a new data set from the same study; to look for causes of discordance among the reported findings; and to try to see if some justifiable level of harmony can be drawn.

STUDY AREA AND LAYOUT

The Desert Experimental Range, a 55,000-acre study area established in 1933, contains a set of twenty 240- or 320-acre grazing paddocks in its south-central portion. The paddocks are in an ecological zone commonly called the "salt-desert shrub" in the Great Basin Desert. We prefer the term "low-shrub cold desert" because the vegetation is generally limited to species approximately a foot or so in height, and the soils are nonsaline in the upper part of the profiles, where nearly all the roots are. The soils are calciorthids, torrifluvents, and occasionally torripsamments. The amount and timing of precipitation varies widely from year to year; the average annual amount is 6 inches. Winters are cold and summers warm. Above-ground vascular plant productivity averages about 250 pounds per acre (Holmgren 1973).

In 1935 each paddock was assigned a grazing treatment which it received annually for 50 years. A treatment is a combination of grazing

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intensity and season of use by sheep. The intensities are light use (an average of 8.5 sheep days per acre), medium use (12 sheep days), and heavy use (17 sheep days). The seasons of use are early winter, middle winter, and late winter. The first two occur during plant dormancy in cold weather; the third includes the period of thawing, warming of soil, and the beginning of plant growth. Some of the paddocks have split seasons of use, such as early-and-middle winter.

Paddock vegetation has been sampled by several different systems (fig. 1). Each 240- or 320-acre paddock has 96 or 128 permanently marked plots, 200-ft² in area, where live-plant cover and production have been periodically estimated at the end of the growing season. Additionally, within each of 16 of the paddocks, two pairs of 1-acre areas were established at the beginning of the study for more intensive observation. One member of each pair was grazed and one was protected from grazing by a fence. These areas, which we will refer to as "special acres," were sampled for cover and production on 40 permanent 200-ft² plots. These plots were sampled less frequently than the paddocks. Also, two 5- by 20-ft chart quadrats were located on each special acre; perennial plants in these quadrats were mapped at irregular intervals. Detailed community-type maps were made for the paddocks in 1935 and again in 1977. Type maps of the special acres were made in 1935 and 1967.

SOME PAST INTERPRETATIONS OF VEGETATION TRENDS

Among reports on the DER paddock grazing study, the period of study being reported has varied;

the earlier ones, of course, covered only part of the period considered in later ones. The dynamic nature of the vegetation, together with time needed for following successional progress, will often result in different community compositions at different times. Other factors involved raise questions regarding the vegetation's actual response to grazing treatments; important among these are (a) variety of purpose, experience, and viewpoint of authors; (2) problems of experimental design and field layout; and (3) the fact that different data sets were used by different investigators (table 1). Here we briefly review varying interpretations of vegetation change reported from the DER grazing study and, based on our own familiarity with the area, offer explanation where possible for part of the conflict or point out insufficiency of data or differing rationale where apparent.

Harper (1959), using quadrat-chart data, concluded that the greater amount of total plant cover mapped in 1958 than in 1935 on the special acres, both grazed and not grazed, was the result of a reduction of grazing pressure from what it had been before the beginning of the study, rather than the result of more favorable moisture conditions. Norton (1978), using a longer period of data from some of the same plots and including the time period covered by Harper, concluded that grazing had little effect on trends in the plant communities and that climate or some other environmental factor was responsible for vegetation change—an opposite interpretation.

Harper's conclusion that, even under the heavy DER grazing treatments, pressure was less than it had been prior to management of grazing cannot be verified. Harper's conclusion, however, was based in part on a very heavily grazed-not grazed comparison on nearby public lands. On the ungrazed part, plant cover increased from 1935 to 1958 in an amount similar to that on the DER. Plant cover on the grazed part decreased suggesting plant cover increases on the grazed part of the DER were a response to reduced grazing pressure.

Norton evaluated 4 years of data (1935, 1958, 1969, and 1975), and noted a "trend" in total amount of plant cover (all species together) between dates of observation, upward in the first and third intervals, and downward in the second. Although the time intervals were 23, 11, and 6 years, the changes were no greater than several of the year-to-year production changes shown in figure 2. (Cover and production have been shown to vary in a similar fashion at the DER [Hutchings and Stewart 1953]). The concept of trend involving a simple change in total plant cover is somewhat different than the concept most often used in range management; compositional makeup of cover usually is the important aspect of trend. No doubt cover

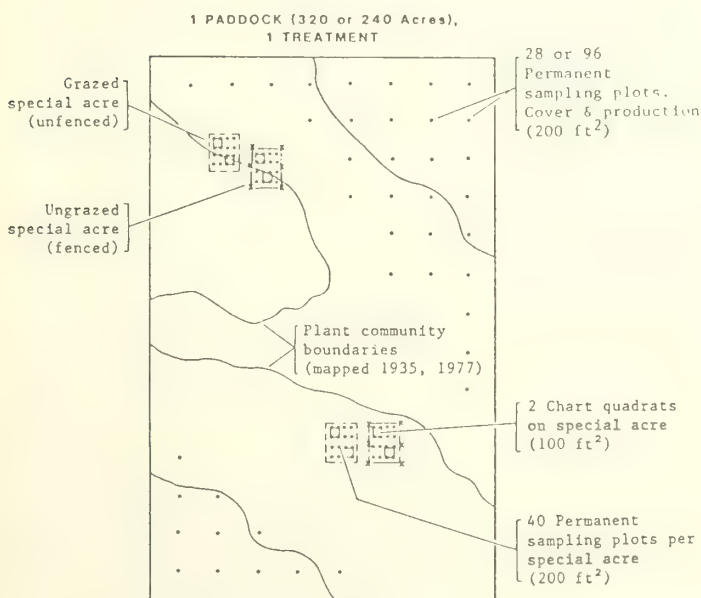


Figure 1.--A representative Desert Experimental Range paddock illustrating the different vegetation sampling systems.

Table 1.--Reports giving differing interpretations of results from the DER paddock grazing study

Report	Data set	Years
Hutchings and Stewart (1953)	Paddock, estimated production	1935 through 1947
Smith (1984)	Paddock, estimated production	1938, 1945, 1957, 1967, 1973
Holmgren and Hutchings (1972)	Paddock, estimated cover	1935 through 1967
Holmgren and Hutchings (1972)	Special acres, estimated cover	1935, 1967
Harper (1959)	Special acres, quadrat chart cover	1935, 1958
Norton (1978)	Special acres, quadrat chart cover, individual plant presence	1935, 1958, 1969, 1975
Chambers (1979)	Special acres, quadrat chart cover, individual plant presence	1975, 1978
West (1979)	Special acres, quadrat chart, individual plant presence	1935, 1936, 1937, 1958, 1968-70
Clary and Holmgren (this paper)	Special acres, estimated cover	1935, 1967, 1983-84

was affected by climate, but the data presented by Norton do show important compositional changes related to grazing treatment that were not identified by the author. Interpretation may be conditioned by experience and viewpoint.

Several authors (Hutchings and Stewart 1953; Holmgren and Hutchings 1972; Smith 1984) have reported major die-offs of shadscale (*Atriplex confertifolia*) during specific drought periods, but another author (Chambers 1979) analyzed plant demographic data bracketing one of these periods and reported a reduction rather than an acceleration in the rate of population change. Her study was of the 1976-77 drought that closely followed the 1971-72 drought. Could earlier plant mortality have affected results in 1971-72 by removing those plants most susceptible to drought?

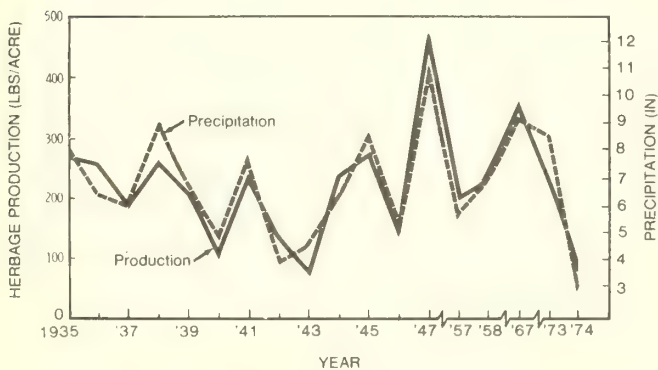


Figure 2.--Relationship of total herbage production to annual precipitation on the Desert Experimental Range.

In a major publication summarizing DER results, Hutchings (Hutchings and Stewart 1953) reported increases in winterfat even under heavy grazing, while in a later publication he reported no change in winterfat under heavy grazing after considering the effect of current year's precipitation (Hutchings 1966). However, by either approach, he found winterfat increased on the moderately and lightly grazed paddocks; these results were significantly different from those of the heavily grazed paddocks. A still later publication coauthored by the same individual reported severe losses of winterfat under heavy grazing in the spring, but gains under heavy fall-winter grazing (Holmgren and Hutchings 1972). Hutchings lumped data different ways in separate analyses. In the earlier publications he grouped pastures by intensity of use, disregarding season of grazing. In the later paper he reported on seasonal effect within intensity groups. The earlier averages or trend lines are composites of what was presented later; that is, the upward trend of winterfat in the early winter heavily grazed pastures combined with the downward trend in the late winter heavily grazed pastures are components of the trend shown for all heavily grazed pastures. So there is no conflict of data in these reported findings, but a change in analysis approach and perhaps a change in viewpoint.

Other results suggest different responses by the same plant species to grazing treatment on different soils, and sometimes to different time periods (Holmgren and Hutchings 1972; Smith 1984). Variables such as grazing intensity and timing, weather, and soils can be expected to interact differently within various plant communities with dissimilar competitive situations.

Is the DER different from other range research areas in difficulty of interpretation? Probably not. The principal difference likely lies in the fact that a number of people have studied vegetation change there over a 50-year period. Thus, the opportunity existed to examine and reexamine assumptions of vegetation change. Few other research areas have been subjected to a similar degree of repeated scrutiny.

What are some of the more obvious reasons for differences in interpretation of vegetation trends on a seemingly uniform area such as the DER? Plant community responses are known to be sensitive to annual precipitation (fig. 2). Obviously, current annual precipitation has to be accounted for in some manner if vegetation trends are to be properly interpreted. Response by individual species to seasonality of precipitation is a very real, but possibly more difficult problem, with timing of soil moisture so unpredictable and so erratic that no "average" pattern is meaningful. For instance, bud sagebrush (*Artemisia spinescens*) with its very restricted spring growth and reproductive period cannot respond to summer rainfall, whereas winterfat (*Ceratoides lanata*) has the ability to respond strongly to summer rainfall. Thus, seasonality of precipitation in the year of observation can substantially affect the apparent dominance within plant compositions. This occurs in plant cover measurements as well as plant production measurements.

Species mortalities may be differentially affected by annual and seasonal drought periods. The reported die-offs of shadscale obviously affected interpretations by different authors when their data sets were from different periods of time. The response of plant composition to release from grazing pressure on the DER has varied strikingly at different locations that appear to be similar, but apparently represent different ecological sites, or variety in attributes such as grazing histories, degree of depletion, and relative abundance of seed source. Since present knowledge does not allow one to differentiate among many of these sites at our study location, they are an obvious source of confusion. Potential interaction of climatic factors, site, and insect attacks also can cause changes that may be erroneously interpreted. The lack of good experimental design in grazing studies initiated 50 years ago has also made proper interpretation more difficult.

SOME RECENT RESULTS

The most recent data from the DER grazing paddocks contribute to a time sequence comparison which is eight to nine years greater in length than any previous comparison and, as such, provide a test of plant trend interpretations of earlier studies. The data were collected on the 200-ft² plots within the 64 paired 1-acre plots for paddocks numbered 1-16. These plots have been studied relatively little during the 50-year history of the DER.

Although incomplete or partial sets of data were obtained in several intermediate years, the only complete sets of data were obtained in 1935, 1967, and 1983-84. The last set was obtained over a 2-year period.

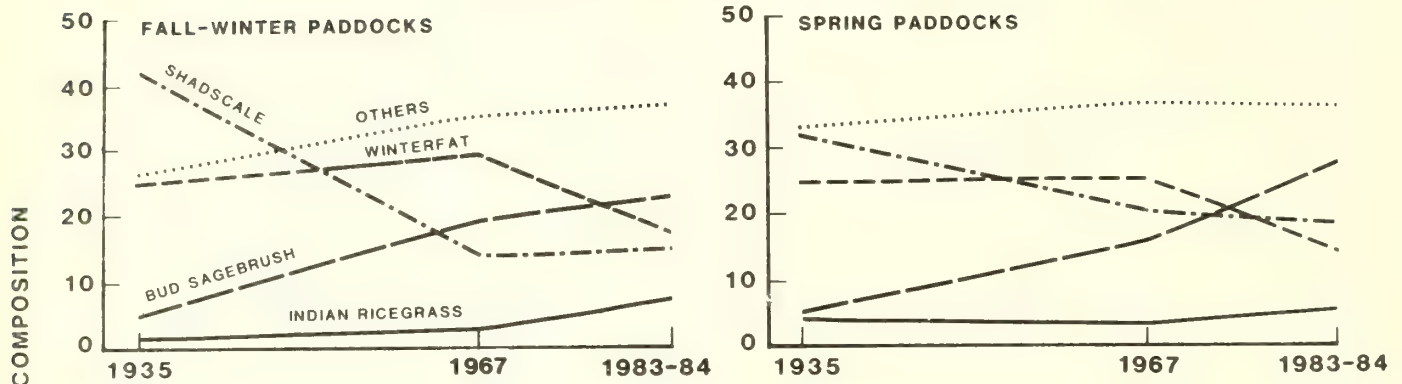
Plant cover data were collected using the square-foot-density method. Plant composition expressed as a percentage of total cover was the basis of analysis, on the assumption that the proportion of total cover for a species is a more stable variable among years than absolute cover. The grazing intensity data were composited for the spring and fall-winter periods to illustrate general trends. Four major species were used to illustrate plant trends: bud sagebrush, winterfat, shadscale, and Indian ricegrass (*Oryzopsis hymenoides*).

Looking at the composited graphs (fig. 3) one can see that the plant composition was quite similar within groups of paired grazed and ungrazed plots in 1935 at the beginning of the study period. The ungrazed portions of both groups illustrate a similar pattern through time: an initial decline followed by a stabilization of shadscale; a slight rise and then a decline of winterfat; an apparently consistent increase in bud sagebrush to a point of community dominance in the early 1980's; and little change to 1967 followed by a modest rise for Indian ricegrass. The "others" category consisted largely of warm season grasses that reacted rather similarly among paddocks with a general increase within the composition.

Under grazed conditions (average of all grazing intensities) substantial differences in response occurred between the spring and fall-winter periods. Spring grazing resulted in a modest overall increase of shadscale in spite of the reported die-offs during dry cycles, and an elimination of bud sagebrush at all grazing intensities studied. Fall-winter grazing appeared to have a reverse effect on these two species. Shadscale experienced a decline through the period of measurement, while bud sagebrush showed little change before 1967, then increased somewhat. Winterfat showed a general decline through the period under both seasons of grazing, while Indian ricegrass showed little change before 1967, but increased later. Under both seasons of grazing each of the latter two species ended up as 10 to 13 percent of the composition.

The decline of winterfat under fall-winter grazing from 1967 to 1983-84 would not have been predicted from earlier results. Several of the researchers mentioned earlier, analyzing data sets spanning the mid-1930's through the late 1960's or early 1970's, reported winterfat increasing in importance under early winter use and under no grazing. Current data, showing substantial reductions in winterfat in the 1980's under all grazing situations including no grazing, suggest causal effects other than grazing (fig. 3). The increase of the spring-growing Indian ricegrass under spring

UNGRAZED SPECIAL ACRES



GRAZED SPECIAL ACRES

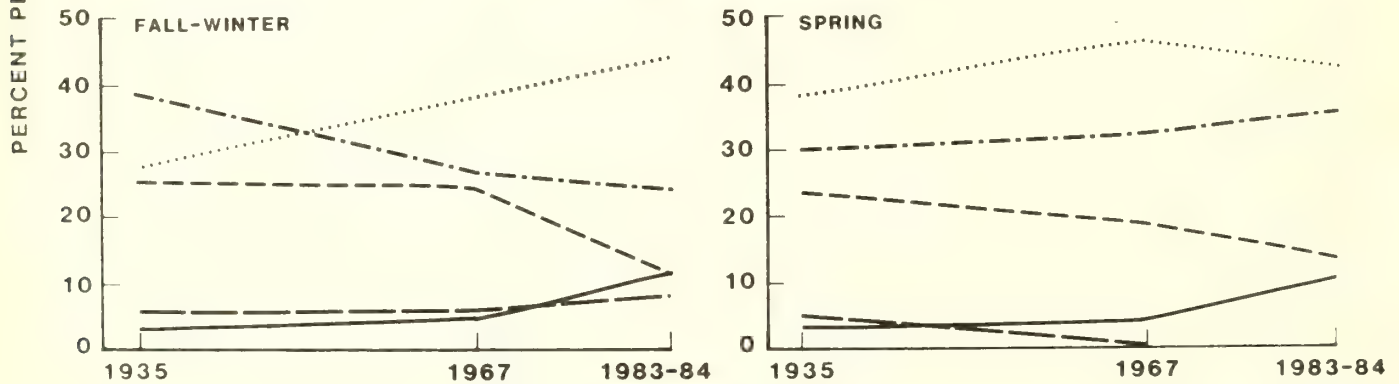


Figure 3.--Proportion of plant cover contributed by four major species and others in paddocks of all grazing intensities.

grazing use would not have been predicted from earlier results either.

As mentioned in the introduction, desert vegetation is dynamic and often reacts to factors other than grazing. The apparent increase in winterfat from 1935 to 1967 was in agreement with other published results (Holmgren and Hutchings 1972). However, precipitation in 1967 was unusual (fig. 4). Not only was the total amount (9.31 in) considerably above average (6.09 in), but most of the increase was in the summer period when winterfat could respond more to an increased moisture supply than could the other three species. Could the apparent increase in importance of winterfat have been due to the distribution of rainfall in 1967 and not to a general compositional trend?

Another of many interesting examples of divergence from anticipated response occurred on the special acres in paddocks 7 and 8 (fig. 5). These two paddocks were heavily grazed during the fall-winter period. The plant composition was determined for paddock 8 in 1983 and for paddock 7 in 1984. Water year 1983 was slightly

drier than average, but the influential factor was the precipitation that occurred in the last week of water year 1982 (fig. 6). This (3.67 in) exceeded one-half of the expected total annual precipitation and was the apparent reason for luxuriant early plant growth the

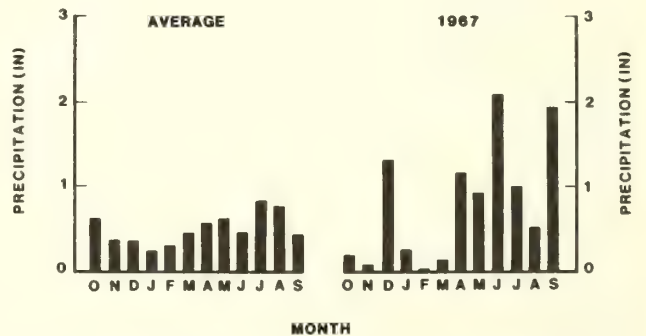


Figure 4.--Amount and monthly distribution of precipitation for water year 1967 and long-term average at the Desert Experimental Range.

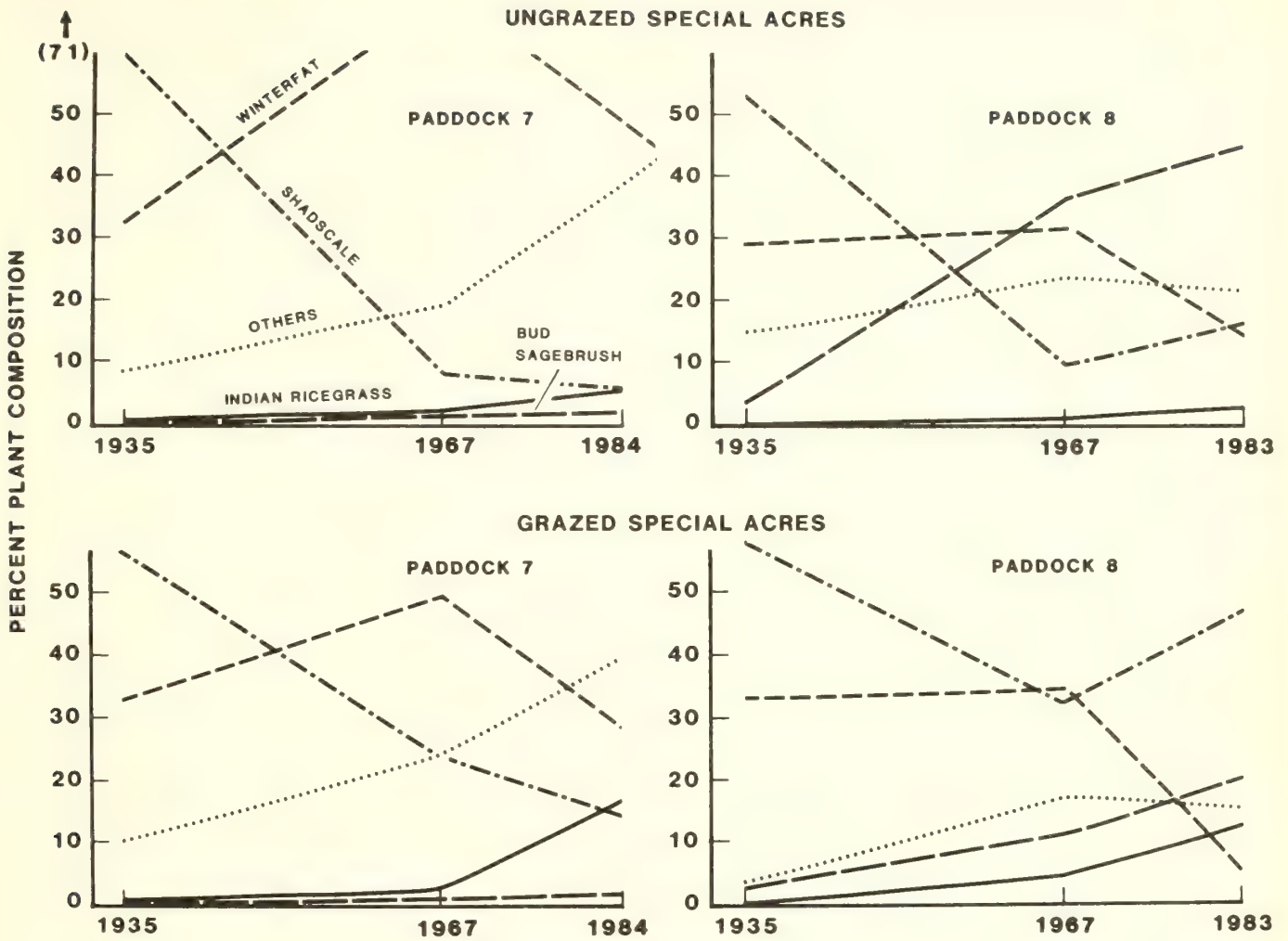


Figure 5.--Proportion of plant cover contributed by four major species and others in paddocks 7 and 8.

spring of 1983 with a strikingly profuse flowering of gooseberryleaf globemallow (*Sphaeralcea grossulariaefolia*) (fig. 7). This moisture supply could have caused an unusual response by the spring-growing shadscale and bud sagebrush. The summer precipitation pattern in

1984 would appear to have benefited winterfat and explain its strong dominance in the 1984 data of paddock 7.

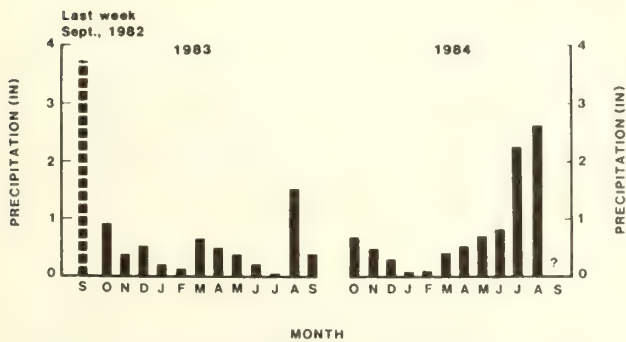


Figure 6.--Amount and distribution of precipitation for water years 1983 and 1984 at the Desert Experimental Range.



Figure 7.--Profuse growth and flowering of gooseberryleaf globemallow and other species the spring of 1983.

Moisture patterns may be the primary reason for apparent plant growth discrepancies, but there are other questions. Let us again look at figure 5. All plots were measured in 1967, therefore all were subject to the same weather patterns. These two paddocks had similar plant compositions in 1935, experienced the same grazing treatments, were located adjacent to one another, had experienced the same weather patterns, and yet were already responding very differently by 1967.

Further examination of information on paddocks 7 and 8 shows that the soils on the 1-acre plot pairs, extracted from small scale maps of the DER (Tew and others no date), were as follows:

Plot pair	Paddock 7	Paddock 8
1	Hiko Springs gravelly sandy loam	Sardo gravelly sandy loam
2	Aysees gravelly sandy loam	Hiko Springs gravelly sandy loam

The most similar responses did not occur between paddock 7 plot 1 and paddock 8 plot 2 as might be expected because of similar soils. Responses were the most similar between plots within paddocks--why? The most apparent reason for this unexpected response was an almost total lack of bud sagebrush on the 1-acre plots of paddock 7 in 1935. Thus, winterfat was able to retain general dominance in paddock 7, while bud sagebrush became dominant on the ungrazed plots and the second most dominant on the grazed plots of paddock 8. Bud sagebrush increased about six times in both paddocks--the main difference was the different starting points; paddock 7 had little more than a trace of bud sagebrush in 1935 while in paddock 8 it represented nearly 4 percent of the plant composition.

Why was bud sagebrush virtually absent from the 1-acre plots of paddock 7 at the beginning of the study period--the only paddock in which that situation occurred? Was the reason insects, disease, early day grazing concentrations, or some undefined soil or site factor? Once the occasion passes it is difficult if not impossible to reconstruct past events. This is a characteristic problem of evaluating long-term data sets.

CONCLUSIONS

It is very easy for all of us to fall into the mental trap of ascribing vegetation change to one or two simplistic factors. Nature, however, is not usually so simple. Some of the major factors that should be considered when relating vegetation reactions to grazing include:

1. Grazing treatment--including duration of years as well as season and

intensity. A much different result may be witnessed if the length of a grazing trial only exceeds the average life span of shadscale compared to one that exceeds the much longer average life span of winterfat. Length of time affects (1) ability of an initially very minor component to eventually express itself; and (2) the likelihood of the low-frequency events that allow recruitment of normally infrequent new plant establishment.

2. Grazing animal species--have the differences in diet selection been fully accounted for?
3. Botanical composition--interspecies competitiveness is too often ignored. A species may actually increase even though it is being grazed during a susceptible period, if its competitors in the plant community are suffering even greater stresses of one form or another.
4. Soil and site--the same species can respond to grazing and to climate differently on different sites. Site is often confounded with treatment.
5. Weather and climate cycles--have these been fully considered when assessing effect of recent grazing management changes? Plant damaging events such as the valley-bottom floods of the mid-1970's on the DER are not predictable, and their occurrence may have to be noted at the time to properly interpret later plant death.
6. Insects and disease--have these been unnoticed agents of change? These in all probability have to be detected at the time of occurrence. One cannot go back through a long-term data set and discover their presence.
7. Realize that all of these factors can interact in different ways.

In addition to the actual biological and physical changes, the subjectivity of the method of attaining data is important. For example, quadrat charts, theoretically an objective technique, give pictures as indicative of the person who maps them as his handwriting. Cover estimates vary not only across years, but even more so as personnel change.

REFERENCES

- Blaisdell, James P.; Holmgren, Ralph C. Managing Intermountain rangelands--salt desert shrub ranges. General Technical Report INT-163. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1984. 52 p.

- Chambers, Jeanne Cecile. The effects of grazing on salt desert shrub species survival during a period of below-average precipitation. Logan, UT: Utah State University; 1979. 101 p. Thesis.
- Harper, Kimball T. Vegetational changes in a shadscale-winterfat plant association during twenty-three years of controlled grazing. Provo, UT: Brigham Young University; 1959. 68 p.
- Hickey, Wayne C., Jr. A discussion of grazing management systems and some pertinent literature (abstracts and excerpts): 1895-1966. Denver, CO: U.S. Department of Agriculture, Forest Service; [no date]. [Unpaged.]
- Holmgren, Ralph C. The Desert Experimental Range: description, history, and program. In: Arid shrublands: Proceedings 3d U.S.-Australia rangelands panel; 1973 March 26-April 5; Tucson, AZ; 1973: 18-22.
- Holmgren, Ralph C.; Hutchings, Selar S. Salt desert shrub response to grazing use. In: Wildland shrubs--their biology and utilization. General Technical Report INT-1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1972: 153-165.
- Hutchings, S. S. Grazing management of salt-desert shrub ranges in the western United States. In: Proceedings 9th International Grassland Congress; 1966: 1619-1625.
- Hutchings, Selar S.; Stewart, George. Increasing forage yields and sheep production on intermountain winter ranges. Circular 925. Washington, DC: U.S. Department of Agriculture; 1953. 63 p.
- Norton, Brien E. The impact of sheep grazing on long-term successional trends in salt desert shrub vegetation of southwestern Utah. In: Hyder, Donald N., ed. Proceedings of the 1st International Rangeland Congress; 1978 August 14-18; Denver, CO. Denver, CO: Society for Range Management; 1978: 610-613.
- Smith, Courtney Bingham. Analysis of grazing effects and site factors in relation to grazing use of salt desert shrub vegetation, Desert Experimental Range, Utah, 1938-1974. Logan, UT: Utah State University; 1984. 198 p.
- Tew, Ronald K.; Hutchings, Selar S.; Holmgren, Ralph C. Soil survey - Desert Experimental Range, Utah. [No date]. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Boise, ID.
- West, Neil E. Survival patterns of major perennials in salt desert shrub communities of southwestern Utah. Journal of Range Management. 32(6): 442-445; 1979.
- West, Neil E. Dynamics of plant communities dominated by chenopod shrubs. International Journal of Ecology and Environmental Science. 8(1): 73-84; 1982.

INFLUENCE OF UNGULATES ON THE DEVELOPMENT OF THE SHRUB UNDERSTORY
OF AN UPPER SLOPE MIXED CONIFER FOREST

Paul J. Edgerton

ABSTRACT: The role of deer and elk in forest succession was investigated in a recently harvested clearcut in the Blue Mountains, OR. Grazing prevented shrub establishment and favored development of grasses and forbs. Abundant shrubs developed within a fenced exclosure. Results suggest that by considering forage and cover requirements in silvicultural plans, managers can utilize ungulate foraging as a vegetation management tool.

INTRODUCTION

Timber harvesting characteristically changes the environment of mixed conifer forests of the interior Pacific Northwest. Disturbance resulting from logging and associated silvicultural practices creates habitats that favor the germination and establishment of numerous understory herbs and shrubs. The seral plant community mosaics that develop in these managed forests differ widely in age, size, distribution, vegetative composition, and structure. They serve as seasonal foraging areas for several kinds of wild ungulates and often livestock.

Traditionally, large ungulates, including mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and Rocky Mountain elk (*Cervus elaphus nelsoni*) have been assigned a largely passive role in the development of forest ecosystems. Managers and biologists have been concerned with balancing animal numbers with available forage, and more recently, with maintaining areas of suitable cover (Thomas 1979). Little attention, however, has been given to the influence of ungulate foraging on the development of seral vegetation and to using that knowledge in the formulation of vegetation management strategies.

A long-term study has been conducted in the Blue Mountains of northeastern Oregon to provide land managers with information on secondary plant succession following timber harvest and residue treatments. This paper presents vegetation data,

collected within and outside a fenced exclosure constructed for that study, that demonstrate the important function of deer and elk grazing on forest succession.

STUDY AREA AND METHODS

The study was conducted within an 8.1-ha clearcut and an adjoining unlogged stand of similar size on the Umatilla National Forest north of La Grande, OR. The area is part of the Mottet Timber Sale (lat. 45°39' N, long. 117°58' W). Elevation is 1 370 m and annual precipitation is estimated at 89-114 cm based on measurements taken at a nearby station (Fowler and others 1979). The growing season is typically warm and dry with most precipitation falling as snow during the fall and winter months. Soils have developed from volcanic ash deposited over residual basalt-derived soils and are 135 cm or more in depth. The slope is moderate and east-facing.

Forest structure and composition are characteristic of maturing mixed conifer forests in the grand fir (*Abies grandis* [Dougl.] Lindl.) zone in the northern Blue Mountains. The unlogged stand is a 175-year-old forest of grand fir, western larch (*Larix occidentalis* Nutt.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). Average tree basal area is 75.0 m²/ha with 94 percent canopy cover.

Ecologically, the study area can be classified as the *Abies grandis*/*Pachistima myrsinites* (Pursh) Raf. habitat type of Daubenmire and Daubenmire (1968) and the white fir (*Abies grandis*/twinflor (*Linnaea borealis* L.)/forb plant community of Hall (1973). As shown in figure 1, understory vegetation cover in the undisturbed forest was relatively high. It included three grasses, 30 forbs, and 10 shrubs but was dominated by a large number of low-growing, shade-tolerant, rhizomatous forbs such as queencup beadlily (*Clintonia uniflora* [Schult.] Kunth), coolwort foamflower (*Tiarella unifoliata* Hook.), and pioneer violet (*Viola glabella* Nutt.). Big whortleberry (*Vaccinium membranaceum* Dougl. ex Torr. in Wilkes) was the only shrub of any importance, and its scattered stems appeared low in vigor.

Logging in the clearcut was completed during the summer of 1964. The forest floor was extensively disturbed by the tractor logging and a considerable

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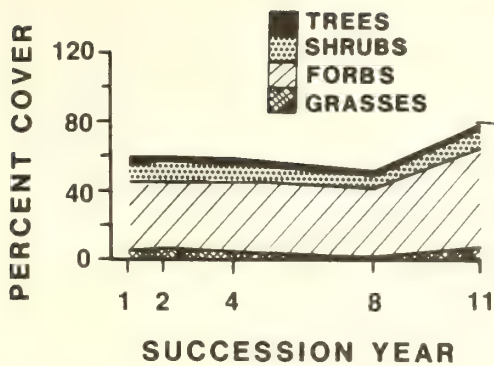


Figure 1.--Understory plant cover in an old-growth mixed conifer stand at the Mottet study area. Cover is expressed as the total layered canopy cover of each plant group and may exceed 100 percent.

amount of slash remained. To facilitate description of seral vegetation development as a result of commonly used residue treatments, one-half of the unit was broadcast burned during the fall of 1965; the remainder of the unit was left untreated. Domestic grasses were seeded on the encircling fireline but not within the unit itself. Seedlings of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Douglas-fir, grand fir, and Engelmann spruce were outplanted during the spring of 1966.

Large herds of elk and scattered, smaller groups of deer utilized the study area and surrounding forest for both forage and cover. Although their length of stay varied from year to year with the depth and persistence of the winter snowpack, animals or their signs were generally observed from early May through late November. Livestock grazed adjacent forest range but were not present within the study area.

Noting that deer and elk foraged heavily on seral vegetation developing in logged areas in nearby forests, we constructed a 1.6-ha enclosure to determine the effects of grazing on plant development and composition. The fenced area straddled burned and unburned treatments near the center of the unit.

Vegetation development was measured as percent cover using the procedure described by Daubenmire (1959). Measurements were taken in late August on 120 0.19-m² permanent plots located in each of the following treatments: unburned and grazed; burned and grazed; unburned and ungrazed; burned and ungrazed. Vegetation in the adjoining unlogged stand was described by the same procedure.

The number of animals utilizing the study area was not determined. An index to use during the initial 4 years of plant succession was provided by annual counts of deer and elk pellet groups on forty-eight 9.3-m² permanent plots in each unfenced treatment in the clearcut and the unlogged area.

The study design is a case history; hence, the data are presented as treatment means for succession years 1, 2, 4, 8, and 11 with no

attempt to make statistical comparisons. In keeping with the focus of this symposium, the response of understory shrubs is emphasized in this paper. A thorough discussion of the development of all seral species at this study site and at companion study sites will be presented in another paper.

RESULTS AND DISCUSSION

Initial Plant Development

Seral vegetation developed rapidly following disturbance. Within 2 years, total vegetation cover in each treatment area of the clearcut (figs. 2 and 3) exceeded that in the unlogged forest understory (fig. 1). Increased light and moisture stimulated growth of surviving understory forbs such as sandwort (*Arenaria macrophylla* Hook.) and sweetscented bedstraw (*Galium triflorum* Michx.). Deeply churned soils and heavily burned spots were extensive and provided environments conducive to the germination and establishment of short-lived forbs such as bull thistle (*Cirsium vulgare* (Savi) Ten.); perennial grasses and sedges, particularly Columbia brome (*Bromus vulgaris* (Hook.) Shear) and Ross sedge (*Carex rossii* F. Boott in Hook.); and seral shrubs and trees such as blueberry elder (*Sambucus cerulea* Raf.), Scouler willow (*Salix scoulerana* Barratt ex Hook.), and western larch.

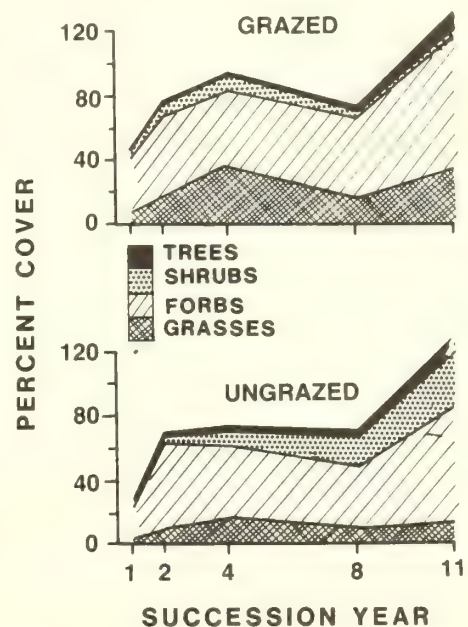


Figure 2.--Plant development in the unburned portion of the clearcut, Mottet study area. Cover is expressed as the total layered canopy of each plant group and may exceed 100 percent.

Animal Use

Pellet group counts (table 1) showed that wild ungulates, particularly elk, used the area extensively during the early years of secondary

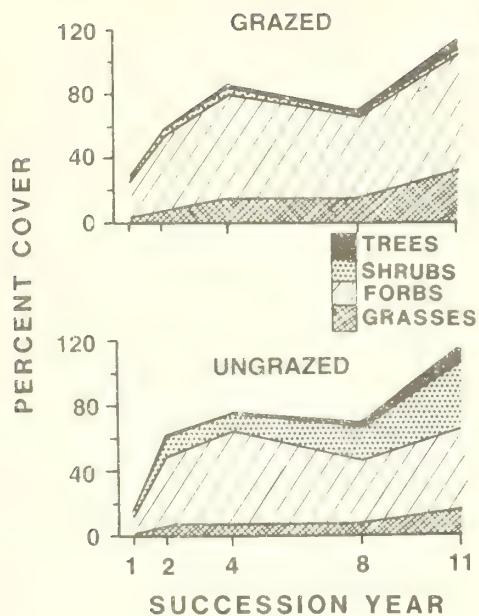


Figure 3.--Plant development in the burned portion of the clearcut, Mottet study area. Cover is expressed as the total layered canopy cover of each plant group and may exceed 100 percent.

succession. Timber sale location facilitated animal use. The unit was located approximately 1 km from the nearest, well-traveled road along a "dead-end" logging spur that was not maintained. Accordingly, as soon as harvest and residue treatment were completed, animals freely moved about the forest with minimal human disturbance.

Similar densities of deer pellet groups were found in the forest and clearcut, but elk pellet groups were more than twice as numerous in the clearcut

Table 1.--Mean annual ungulate use of the Mottet study area as determined by pellet group counts during the first 4 years following timber harvest

Treatment	Deer	Elk
	-- <u>Pellet groups/ha</u> --	
Unlogged forest	174	270
Unburned clearcut	152	646
Burned clearcut	174	652

as in the forest. These data may not, however, be a reliable index to habitat preference. Reports evaluating pellet group sampling show that activities, such as resting and foraging, are often habitat-related and may result in large variations in defecation rate (Collins and Urness 1981; Skovlin 1982). Nonetheless, it seems logical to assume that elk spent a large proportion of the time foraging in the clearcut. They also foraged in the forest, but numerous encounters with bedded animals suggest it provided essential thermal and hiding cover between foraging periods.

Grazing Effects

Figures 2, 3, and 4 allow comparison of the development of grazed versus ungrazed seral forest communities. Although grazing was noted on most plant species, its major impact was to prevent the development of shrubs while promoting the growth of grasses and sedges. Grazing obviously played a controlling role in determining vegetation composition and structure. Use was noted on many plant species, but shrubs showed the greatest impact. Seedlings of 10 species occurred throughout the clearcut during the initial 1 to 3



Figure 4.--Photos of seral forest communities in grazed versus ungrazed portions of the Mottet clearcut. A--burned portion after 11 seasons of grazing. B--burned portion after 11 seasons of protection. The abundant, low-growing shrubs near the center of photo B are myrtle pachistima. The taller shrubs are Scouler willows.

years after disturbance, but those accessible to deer and elk were soon heavily browsed. Repeated removal of most leaves, current twig growth, and portions of the woody stems prevented establishment and growth. By the fourth or fifth season, only those scattered, individual shrubs partially protected from overuse beneath logs or within slash piles survived. Total shrub cover averaged just 2.6 percent in the burned area and 3.7 percent in the unburned treatment after 11 years of grazing.

The photo (fig. 4a) of the area outside the enclosure illustrates the grass-forb understory that developed as a result of grazing. Composition was diverse: 11 grasses, 51 forbs, and nine shrubs in the unburned area, and 10 grasses, 40 forbs, and 10 shrubs in the burned portion. Abundant species included Columbia brome, Ross sedge, western coneflower (*Rudbeckia occidentalis* Nutt.), lanceleaf figwort (*Scrophularia lanceolata* Pursh), and bracted strawberry (*Fragaria vesca bracteata* [Heller] Davis. Although production of preferred shrubs had been greatly reduced by grazing, this diverse understory provided an abundance of forage until shade of the rapidly developing conifer crowns became the controlling factor.

Within the enclosure, absence of animal use favored the development of shrub seedlings. After 11 years, shrub cover totaled 35 percent in the burned portion and 41 percent in the unburned portion as compared to less than 4 percent in each of the grazed areas. In contrast, total grass and sedge cover within the enclosure was approximately one-half that occurring outside.

Twelve species of shrubs occurred within the enclosure. Several species such as baldhip rose (*Rosa gymnocarpa* Nutt.) and common snowberry (*Symphoricarpos albus* [L.] Blake) were scattered in the understory of the unlogged forest (table 2) and may have sprouted from rootstalks. Most seral shrubs were observed, however, to develop from new seedlings. Major differences in composition between treatments were expected because burning (heat) favors the germination of several widely occurring seral forest shrubs such as snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex Hook.) (Conard and others 1982). Surprisingly, ceanothus was a minor seral species in both the unburned and burned portions of the clearcut (table 2). Myrtle pachistima (*Pachistima myrsinites* [Pursh] Raf.) was the only shrub whose establishment apparently benefitted from slash burning. This low-growing, evergreen shrub is found throughout the Blue Mountains but is rarely a major understory component in forest communities grazed heavily by wild and domestic ungulates. Only scattered pachistima shrubs (average cover <0.05 percent occurred in the unlogged forest. Since the seeds of this species are not carried by the wind and adjacent seed sources are not available for distribution by animals, one might speculate that the numerous seedlings found in the burned portion germinated from buried seed deposited by shrubs present during an earlier successional period.

Several individuals of black cottonwood (*Populus trichocarpa* Torr. I Gray) developed in the enclosure and exceeded 4 meters in height after 11 years. These deciduous trees are usually restricted to riparian environments and are not

Table 2.--Shrub cover in the Mottet clearcut study area 11 seasons after logging disturbance

	Burned clearcut		Unburned clearcut		Unlogged grazed
	Grazed	No grazing	Grazed	No grazing	
	-----Percent cover-----				
<u>Amelanchier alnifolia</u> Nutt.	--	--	--	--	0.2
<u>Berberis repens</u> Lindl.	--	--	--	--	tr ¹
<u>Ceanothus velutinus</u> Dougl. ex Hook.	--	1.7	tr	--	--
<u>Chimaphila menziesii</u> (R. Br.) Spreng.	--	--	--	--	0.2
<u>Chimaphila umbellata</u> (L.) Bart.	--	--	--	--	0.6
<u>Holodiscus discolor</u> (Pursh) Maxim.	--	--	0.3	--	--
<u>Lonicera utahensis</u> Wats.	--	--	--	tr	--
<u>Pachistima myrsinites</u> (Pursh) Raf.	0.6	19.1	--	3.3	tr
<u>Prunus emarginata</u> (Dougl.) Walpers	--	0.3	--	--	--
<u>Ribes lacustre</u> (Pers.) Poir. in Lam.	0.3	4.6	0.3	9.8	0.1
<u>Ribes viscosissimum</u> Pursh	0.7	6.8	0.3	4.9	--
<u>Rosa gymnocarpa</u> Nutt.	0.4	--	0.2	3.5	0.2
<u>Rubus parviflorus</u> Nutt.	0.2	2.6	1.5	3.4	--
<u>Salix scoulerana</u> Barratt ex Hook.	--	6.3	--	4.6	--
<u>Sambucus cerulea</u> Raf.	tr	tr	0.9	2.6	--
<u>Sorbus scopulina</u> Greene	--	--	--	--	0.1
<u>Symphoricarpos albus</u> (L.) Blake	0.3	--	tr	1.8	0.2
<u>Taxus brevifolia</u> Nutt.	--	--	--	--	7.6
<u>Vaccinium membranaceum</u> Dougl. ex Torr. in Wilkes	0.1	--	0.2	0.7	3.0
Total shrub cover	2.6	41.4	3.7	34.6	12.2

¹ tr = trace (<0.1 percent cover)

found in nearby forest stands; it is likely they developed from seeds widely dispersed by wind.

Establishment and growth of trees in recently harvested areas are major concerns of forest managers. In these forests, clearcut units must be satisfactorily restocked with young trees within 5 years after final disturbance. At the Mottet study area, a survey 2 years after planting showed that 7.3 ha (90 percent) of the unit was satisfactorily stocked with at least 618 trees/ha. After 11 seasons, stocking averaged 3,258 trees/ha for the entire unit. Grand fir, Engelmann spruce, and Douglas-fir occurred both as planted and naturally regenerated species. Western larch consisted entirely of seedlings established from natural seedfall. Minimal browsing or trampling damage of seedlings was noted at any time during the study.

Table 3 compares tree establishment and growth in grazed versus ungrazed vegetation that developed in the burned portion of the clearcut. Comparable data for the unburned treatment are not presented because portions of that treatment were not planted. Data for the burned area suggest that grazing was compatible with tree regeneration and may have benefited both establishment and growth. Other investigators in the Pacific Northwest have reported increased tree growth where competing understory vegetation has been reduced by carefully managed livestock grazing (Krueger 1983; Richmond 1983).

Table 3.--Stocking and height of conifers in the burned portion of the Mottet study area 11 seasons after disturbance

Species	Grazed	No grazing
<u>---Mean number trees/ha---</u>		
Grand fir	1640	1363
Western larch	1195	929
Douglas-fir	889	128
Engelmann spruce	395	336
Ponderosa pine	59	198
Total	4178	2954
<u>---Mean height (cm)---</u>		
Grand fir	156.0	140.1
Western larch	290.4	264.0
Douglas-fir	283.5	166.2
Engelmann spruce	162.9	191.4
Ponderosa pine	317.7	320.7

CONCLUSIONS AND IMPLICATIONS

This study has clarified the important functional role that deer and elk foraging plays in secondary succession in forests of the interior Pacific Northwest. Deer and elk altered both the pace and direction (composition) of the development of early stages of the forest succession model presented by Thomas (1979). Grazing prolonged the initial grass-forb stage while preventing shrubs from developing as the major component of the understory during seedling and sapling stages.

These effects have also been observed to be important factors influencing the composition of the understory of later successional stages. This is evidenced by Hall's (1973) description of the white fir-twinflower-forb forest community; he stated that "shrubs are conspicuously absent or very restricted in occurrence." It is obvious that patterns of past and present animal use are important factors to consider when classifying plant communities and characterizing ecosystem processes in these forests.

Knowledge of the effects of ungulate grazing on forest succession has important implications for the formulation of vegetation management strategies that may affect timber, watershed, and wildlife habitat values. During early successional stages, grazing either by wild ungulates or livestock has the potential to alter the composition and reduce the biomass of shrubs and other understory vegetation that may compete with tree seedlings for light, moisture, and nutrients. However, ungulate grazing may negatively impact watershed characteristics, not only by altering plant cover but also by causing soil compaction and surface disturbance on sensitive soils (Gifford 1981). Further, reduction in the number and size of seral shrubs simplifies understory structure and may have long-term impacts on habitat quality for dependent species of nongame wildlife (Balda 1975).

Planned or unplanned, forest harvests and other silvicultural activities create mosaics of forage and cover areas that strongly influence the distribution and degree of ungulate grazing. By understanding and considering animal needs, managers have opportunities to manipulate the size, arrangement, and structure of habitats to either minimize grazing influence or utilize it as a subtle but effective vegetation management tool.

REFERENCES

- Balda, Russell P. Vegetation structure and breeding bird diversity. In: Smith, Dixie R., ed. Symposium on management of forest and range habitats for nongame birds: Proceedings; 1975 May 6-9; Tucson, AZ. Gen. Tech. Rep. WO-1. Washington, DC: U.S. Department of Agriculture, Forest Service; 1975: 59-80.
- Collins, W. B.; Urness, P. J. Habitat preferences of mule deer as related by pellet-group distribution. *Journal of Wildlife Management*. 45: 969-972; 1981.
- Conard, Susan G.; Jaramillo, Annabelle E.; Cromack, Kermit Jr.; Rose, Sharon, compilers. The role of the genus Ceanothus on western forest ecosystems. Report of a workshop, 1982 November 22-24; Corvallis, OR. Gen. Tech. Rep. PNW-182. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985. 72 p.
- Daubenmire, R. A canopy-coverage method of vegetational analysis. *Northwest Science*. 33: 43-64; 1959.
- Daubenmire, R.; Daubenmire, J. B. Forest vegetation of eastern Washington and northern Idaho. *Tech. Bull.* 60. Pullman, WA: Washington Agricultural Experiment Station; 1968. 104 p.
- Fowler, W. B.; Helvey, J. D.; Johnson, C. Baseline climate and hydrologic relationships for the High Ridge evaluation area. Gen. Tech. Rep. PNW-91. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1979. 17 p.
- Gifford, Gerald F. Watershed responses to grazing management. In: Baumgartner, David M., comp. and ed. Symposium on Interior west watershed management: Proceedings; 1981 April 8-10; Spokane, WA. Pullman, WA: Washington State University; 1983: 147-159.
- Hall, Frederick C. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. Region 6 Area Guide 3-1. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region; 1973. 62 p.
- Krueger, William C. Cattle grazing in managed forests. In: Roche, Ben F., Jr.; Baumgartner, David M., comps. and eds. Symposium on forestland grazing: Proceedings; 1983 February 23-25; Spokane, WA. Pullman, WA: Washington State University; 1983: 29-41.
- Richmond, Robert M. Problems and opportunities of forestland grazing in the Pacific Northwest. In: Roche, Ben F., Jr.; Baumgartner, David M., comps. and eds. Symposium on forestland grazing: Proceedings; 1983 February 23-25; Spokane, WA. Pullman, WA: Washington State University; 1983: 71-73.
- Skovlin, Jon M. Habitat requirements and their evaluations. In: Thomas, Jack Ward; Toweill, Dale E., eds. *Elk of North America: ecology and management*. Harrisburg, PA: Wildlife Management Institute and Stackpole Books; 1982: 369-413.
- Thomas, J. W., ed. *Wildlife habitats in managed forests--the Blue Mountains of Oregon and Washington*. Handbook 553. Washington, DC: U.S. Department of Agriculture; 1979. 512 p.

EFFECTS OF LIVESTOCK GRAZING AND THINNING
OF OVERSTORY TREES ON UNDERSTORY WOODY PLANTS

Daniel W. Uresk

ABSTRACT: Two cultural treatments were employed and evaluated over 7 years to determine their effect on height increases of woody plants in decadent woodlands of southwestern North Dakota. Cultural treatments included exclusion of livestock and removing 40 percent of low-vigor trees. Shrub heights varied with species and cultural treatment. Saskatoon serviceberry (Amelanchier alnifolia), green ash (Fraxinus pennsylvanica), and Woods rose (Rosa woodsii) were taller when livestock were excluded. Green ash was taller where decadent overstory trees were removed. The response of woody plants to these cultural treatments was slow for some species and nonexistent for others.

INTRODUCTION

Woodlands on the northern High Plains are important to livestock and wildlife because they provide shade, thermal cover, and relief from wind and insects (Severson and Boldt 1978; Bjugstad and Girard 1984; Kauffman and Krueger 1984). Many woody plants provide forage during the grazing season (Holechek and others 1982; Roath and Krueger 1982; Uresk and Lowry 1984; Uresk and Paintner 1985). However, heavy grazing by livestock can result in decreased vigor of plants (Garrison 1953; Ellison 1960; Willard and McKell 1978) and alteration of species composition.

Many High Plains woodlands are becoming decadent, nearing the end of their lifespans (Boldt and others 1978), and are being replaced by grassland. These woodlands may require specific management to maintain or enhance their value for livestock and wildlife. Partial removal of the overstory trees on woodlands (increased light; less competition) influences understory production and growth of woody plants (Ehrenreich and Crosby 1960; Jameson 1963). Some woody plants have responded to grazing and tree removal (Boldt and others 1978).

The objectives of this study were to evaluate the effects of (a) livestock grazing and (b) cutting of trees on growth of understory woody plants on the northern High Plains.

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STUDY AREA AND METHODS

The study was conducted over a 7-year period from 1975 to 1981 on the Little Missouri National Grasslands, Custer National Forest, in southwestern North Dakota. A woodland system was selected in the upper reaches of Magpie Creek drainage near Belfield, ND. Trees in these prairie drainages were green ash (Fraxinus pennsylvanica) and American elm (Ulmus americana). The shrub understory included western snowberry (Symphoricarpos occidentalis), Woods rose (Rosa woodsii), spiny currant (Ribes setosum), Saskatoon serviceberry (Amelanchier alnifolia), silver buffaloberry (Shepherdia argentea), common chokecherry (Prunus virginiana), American plum (Prunus americana), hawthorn (Crataegus spp.), and raspberry (Rubus spp.).

Woodlands selected for study were located in two pastures grazed by cattle in a three-pasture range allotment under a deferred rotation grazing system. Stocking rate was 1.07 AUM/ha (animal unit months) from May 15 to October 30. Utilization of forage by late August or early September averaged 35 percent. At the beginning of this study, pastures had been managed for 2 years under this system. Before the deferred rotation grazing system was implemented, the area had been grazed season-long as a single pasture.

Twelve sample sites (0.08 ha each) were selected at scattered locations throughout a major woody draw system where site and vegetation conditions were reasonably uniform and representative (Boldt and others 1978). The experiment included two factors in a factorial design--cattle grazing versus no grazing, and tree removal versus no tree removal. The four treatment combinations were allocated at random on the 12 sites, with three replications per treatment. Fences to exclude cattle were installed in late summer and fall of 1975.

Seven species of trees and shrubs were studied over the 7-year period. These included; green ash, American elm, western snowberry, woods rose, spiny currant, Saskatoon serviceberry and common chokecherry which were common on the study areas. Other wooded species were rare on the sites.

Plots designated for tree removal (green ash; American elm) were selectively cut (40 percent of total stems) to open the canopy and stimulate sprouting in 1975 (Boldt and others 1978). Tree stems were cut to approximately 15-cm stump height

and were removed from the site. The trees with low vigor and poorest of the growing stock as described by Boldt and others (1978) were removed. Pretreatment measurements were collected on all sites. All small live trees were measured for height (< 2.5 cm d.b.h.). Heights of all shrubs and small trees were measured on five belt transects 15.3 m by 1.2 m randomly located on each site. Height measurements (centimeters), were recorded on all sites (one sample period) during late August and early September of each year for 6 years after treatment.

Shrub height measurements were averaged by species and by site for statistical analyses. Analysis of covariance, with pretreatment data as the covariate, was employed to test treatment effects separately for each species each year (Nie and others 1975). When the covariate was not significant ($\alpha = 0.10$), an analysis of variance was used to test for treatment differences. A Bonferroni criterion of $\alpha = 0.04$ was used for individual species and year combinations. This α level was derived from an overall level of $0.25/6$ years for each species (Miller 1961). However, when individual years are considered without the α level divided by 6 many more differences occur, thus the term biological trend is used in the text. The absence of interactions indicated treatments responded independently.

RESULTS

Heights of Saskatoon serviceberry were statistically greater on ungrazed compared to grazed sites during the fourth and fifth years after initial treatment (fig. 1). However, height trends (biological) from the second to sixth year indicate greater heights on the ungrazed treatment. A reduction in the number of overstory trees did not influence heights of serviceberry.

Green ash heights were statistically greater on the ungrazed than on grazed sites in the third, fourth, and sixth years after initial treatment (fig. 1). This indicates that cattle were eating green ash when not excluded from woodlands. Removal of overstory trees resulted in a significant increase in height of green ash from the third through the sixth year.

Height trends for common chokecherry were irregular, with no consistent differences between grazed and ungrazed treatments (fig. 1). However, removal of overstory trees resulted in a general but not significant trend of greater heights throughout the 6-year period.

Spiny currant plants showed no statistical differences in heights between ungrazed and grazed areas throughout the 6 years (fig. 1). However, some indications of biological trends are shown from the third through the sixth year between grazing treatments. Heights were not significantly greater on the uncut tree sites throughout the 6 years, although trends indicate that plants on the uncut site were taller.

Woods rose was taller during the fifth and sixth years on areas where livestock were excluded

(fig. 1). Other years showed no differences in heights between treatments. Woods rose was significantly taller on the sites where trees were not removed than on sites with trees removed only in the second year. All heights of Woods rose were similar between treatments for the remaining 4 years when trees were removed.

Western snowberry was significantly shorter the second year on the ungrazed treatment (fig. 1). No differences were found throughout the remainder of the study. Some evidence of a trend was shown from the third through the sixth year for taller plants on the ungrazed treatment. No differences were observed for heights of snowberry as related to removal of overstory trees.

Heights of American elm saplings generally were not statistically different but were consistently higher on the ungrazed sites when compared to the grazed sites (fig. 1). Height trends for American elm were similar regardless of whether trees were removed. Taller plants were observed on the tree removal treatment, but this was not statistically different.

DISCUSSION

Height response of understory woody plants to grazing and removal of overstory trees was slow. Generally, exclusion of livestock was associated with increased height of Saskatoon serviceberry, green ash, and Woods rose. The other four species showed no response. These differences may be related to the seasonal use of woody plants by livestock (Holechek and others 1962; Uresk and Lowry 1984; Uresk and Paintner 1985). The lack of response differences between grazed and ungrazed treatments may be the result of growth stimulated by herbivore use or the lack of use (Ellison 1960; Jameson 1963).

Thinning overstory trees produced mixed results. Only heights of green ash were taller on the cut treatment. The most abundant shrub, western snowberry, did not respond to removal of overstory trees, nor did the other woody plants. Trends were evident for some species, but they were not statistically significant.

Reduced competition for light, space, and nutrients after cutting large trees may have helped ash seedlings and saplings to grow taller. Ehrenreich and Crosby (1960) reported higher production for understory plants within a hardwood forest as crown cover decreased. However, the plant species responded differently to changes in hardwood crown cover. Pase (1958), working in a ponderosa pine forest, showed that shrub production was greatest when crown canopy cover was from 0 to 19 percent. This was closely followed by shrub production in the 20 to 39 percent canopy cover. Production greatly decreased when canopy cover increased. In this study, forest canopy cover was about 58 percent on the cut sites.

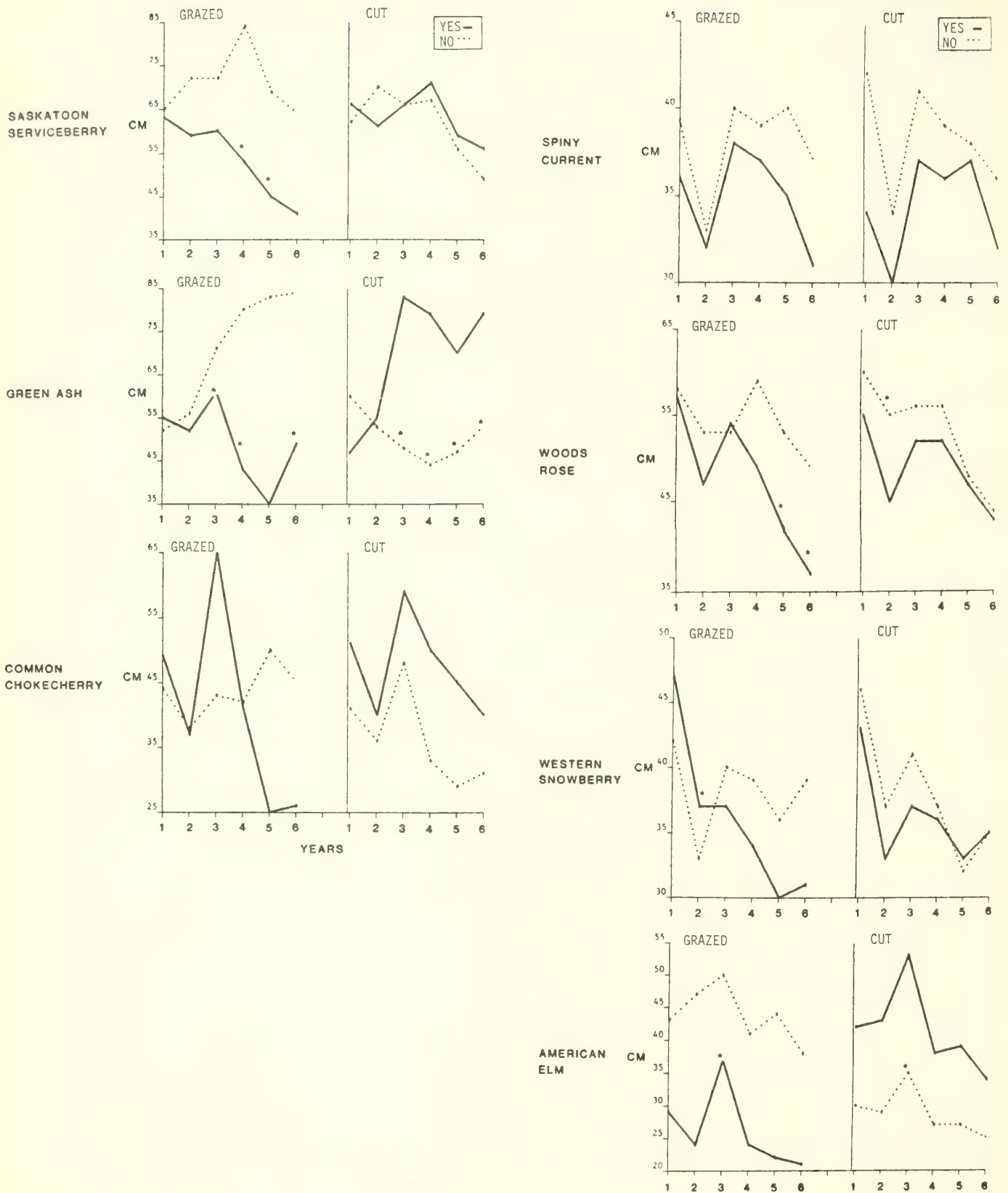


Figure 1.--Response of woody plants (cm) over a 6-year period on grazed (Yes) or ungrazed (No) pastures with 40 percent overstory trees removed (Yes) or 0 percent overstory removed (No). *Treatments are significantly different at $\alpha = 0.04$.

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REFERENCES

- Boldt, C. E.; Uresk, D. W.; Severson, K. Riparian woodlands in jeopardy on northern High Plains. In: Johnson, R. R., and McCormick, J. F., eds. Strategies for protection and management of floodplain wetlands and other riparian ecosystems; Proceedings of symposium, 1973 December 11-13; Calloway Gardens, GA. Gen. Tech. Rep. WO-12. Washington, DC: U.S. Department of Agriculture, Forest Service; 1978: 184-189.
- Bjugstad, A. J.; Girard M. Wooded draws in rangelands of the northern Great Plains. In: Henderson, F. R., ed. Guidelines for increasing wildlife on farms and ranches. Manhattan, KS: Kansas State University Cooperative Extension Service; 1984: 27B-36B.
- Carmer, S. G. Optimal significance levels for application of the least significant difference in crop performance trials. *Crop Sci.* 16: 95-99; 1976.
- Ellison, L. Influence of grazing on plant succession on rangelands. *Bot. Rev.* 26: 1-78; 1960.
- Ehrenreich, J. H.; Crosby, J. S. Herbage production is related to hardwood crown cover. *J. For.* 58: 564-565; 1960.
- Garrison, G. A. Effects of clipping on some range shrubs. *J. Range Manage.* 6: 309-317; 1953.
- Holechek, J. L.; Vavra, M.; Skovlin, J.; Krueger, W. C. Cattle diets in the Blue Mountains of Oregon. II. Forests. *J. Range Manage.* 35: 239-242; 1982.
- Jameson, D. A. Response of individual plants to harvesting. *Bot. Rev.* 29: 532-594; 1963.
- Kauffman, J. B.; Krueger, W. C. Livestock impacts on riparian ecosystems and streamside management implications... a review. *J. Range Manage.* 37: 430-437; 1984.
- Miller, R. G., Jr. Simultaneous statistical inference. 2nd ed. New York: Springer-Verlag; 1981. 299 p.
- Nie, N. H.; Hull, C. H.; Jenkins, J. G.; Steinbrenner, K.; Bent, D. H. SPSS: statistical package for the social sciences. 2nd ed. New York: McGraw-Hill; 1974. 675 p.
- Pase, C. P. Herbage productions and composition under immature ponderosa pine stands in the Black Hills. *J. Range Manage.* 11: 238-243; 1958.
- Roath, L. R.; Krueger, W. C. Cattle grazing influence on a mountain riparian zone. *J. Range Manage.* 35: 100-103; 1982.
- Severson, K. E.; Boldt, C. E. Cattle, wildlife, and riparian habitats in the western Dakotas. In: Management and use of northern Plains rangeland proceedings: regional rangeland symposium; 1978 February 27-28; Bismarck, ND. North Dakota State University, Dickinson; 1978: 90-103.
- Uresk, D. W.; Lowrey, D. G. Cattle diets in the Central Black Hills of South Dakota. In: Proceedings, symposium on wooded draws; 1984 June 12-13; South Dakota School of Mines and Technology Media Center, Rapid City, SD. 1984: 50-52.
- Uresk, D. W.; Paintner, W. W. Cattle diets in a ponderosa pine forest in the northern Black Hills. *J. Range Manage.* 38: 440-442; 1985.
- Willard, E. E.; McKell, C. M. Response of shrubs to simulated browsing. *J. Wildl. Manage.* 42: 514-519; 1978.

USING TWIG DIAMETERS TO ESTIMATE BROWSE
UTILIZATION ON THREE SHRUB SPECIES IN SOUTHEASTERN MONTANA

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ABSTRACT: Browse utilization estimates based on twig length and twig weight were compared for skunkbush sumac, wax currant, and chokecherry. Linear regression analysis was valid for twig length data; twig weight equations are nonlinear. Estimates of twig weight are more accurate. Problems encountered during development of a utilization model are discussed.

INTRODUCTION

One important aspect of managing large herbivore populations in the United States is the ability to estimate utilization of forage species. As development continues to crowd wildlife species, managing herbivore populations to maintain balance in the ecosystem has become a significant issue. Just as livestock managers should maintain proper use in pastures, game managers should strive to maintain game populations at levels that do not abuse the forage resources. Thus, managers need fast and efficient methods of estimating forage abundance and utilization.

Data on both the amount of forage available and the amount removed are needed to estimate utilization. Techniques have been developed whereby both of these parameters can be estimated from data collected in the spring after browsing has occurred. Relationships of twig diameter to weight and length have been developed for a number of shrub species (Telfer 1969; Lyon 1970; Peek and others 1971). Twig diameter-length and diameter-weight relationships have been shown to vary statistically among sites, shrub species, individual plants, and location on the shrub (Basile and Hutchings 1966; Lyon 1970; Peek and others 1971; Jensen and Urness 1981). However, variations among plants, location on the shrub, and to some extent site differences are of little practical value for estimating utilization (Basile and Hutchings 1966; Lyon 1970). Jensen and Urness (1981) showed that utilization on bitterbrush (*Purshia tridentata*) and cliffrose (*Cowania stansburiana*) could be estimated by a series of twig diameter measurements alone. Provenza and Urness (1981) demonstrated that branch and twig diameters could be used to estimate utilization on

blackbrush (*Coleogyne ramosissima*) more accurately than measurements taken before and after browsing. Estimates of utilization based on twig diameter measurements can reduce the number of field trips necessary, and accurate estimates of utilization can be made after browsing has occurred (Jensen and Urness 1981).

The objectives of this study were: (1) to develop models from which estimates of utilization of three shrub species based on twig diameter-length and twig diameter-weight relationships could be made, and (2) to compare browse utilization estimates based on twig length with estimates based on twig weight.

METHODS

This study was conducted about 6 km north of Decker, MT, during the fall of 1984 and spring of 1985. Three shrub species, skunkbush sumac (*Rhus trilobata*), wax currant (*Ribes cereum*), and chokecherry (*Prunus virginiana*), were selected for study. Ten shrubs of each species were identified, and 10 twigs on each shrub were selected and marked for sampling. Twigs were selected randomly, but also to represent the full range of current year's growth. Diameters of five twigs on each shrub were measured at the budscale scar and at a point between the budscale scar and terminal bud. Values were recorded to the nearest 0.1 mm. The length from each of the diameter measurements to terminal bud of the twig was also measured. On the other five twigs, twig diameter was measured at the budscale scar and at a point between the budscale scar and the terminal bud. The twig was then clipped at both measurement points, oven-dried at 60 °C for 3 days, and weighed. These measurements provided 100 data points from which to develop the regression equations to predict twig length and twig weight for each species.

Regression models of the form $Y = a + bX$ (where Y = twig length and X = twig diameter) were developed for twig diameter-length relationships using SPSS New Regression (Hull and Nie 1981). Twig diameter-weight relationships were estimated using the SPSS nonlinear regression subprogram (Robinson 1984) for the model $Y = aX^b$ (where Y = twig weight and X = twig diameter). Residuals were analyzed using SPSS New Regression.

Herbivore utilization was examined in the spring on 35 skunkbush sumac, 13 wax currant, and 18

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chokecherry plants. On each shrub, a small number of twigs on one branch were selected randomly. Diameters of browsed twigs were measured at the budscale scar and browse point with calipers, and total number of browsed twigs were counted. Utilization estimates were determined from mean diameters by plant species.

RESULTS AND DISCUSSION

Utilization Estimates

Examination of twig diameter-twig length data indicated that linear regression analyses (fig. 1) were appropriate for the three shrub species. The regression fits for twig diameter-length relationships from this study were similar to those reported for bitterbrush (Basile and Hutchings 1966) and bitterbrush and cliffrose (Jensen and Urness 1981), but less precise than those Lyon (1970) reported for serviceberry (*Amelanchier alnifolia*). Previous browsing activity, plant vigor, and age contributed to the variation in twig diameter-length data for chokecherry in this study, especially at the larger twig diameters.

The relationships between twig diameter and twig weights for all three species were nonlinear (fig. 2). The equations developed to predict twig weights for skunkbush sumac and wax currant were very similar (table 1). These two species exhibited similar patterns of twig growth. The nonlinear regression equations for twig diameter-weight relationships for all three species had substantially higher regression fits than did linear estimates of twig diameter-weight relationships. Ruyle and others (1983) and Telfer (1969) reported nonlinear equations for twig diameter-weight relationships. Peek and others (1971) reported high correlation coefficients for twig diameter-weight relationships for most species, and Lyon (1970) indicated that the nonlinear relationship (log transformation) between twig diameter and twig weight did not result in any improvement over the linear model.

Estimates of percent utilization based on twig weights were 24, 41, and 52 percent less than estimates based on twig lengths for skunkbush sumac, chokecherry, and wax currant, respectively (table 2). These differences result from the curvilinear relationships between twig weight and twig diameter. The longer and larger twigs had a greater portion of the total weight in the proximal portions of the twig. Browsing at the end of a twig could result in substantial removal of twig length with less proportional removal of twig weight. Therefore, estimates of twig weight are a more accurate index of utilization. Provenza and Urness (1981) also reported less utilization of browse when twig or branch weight estimates were used, compared to twig or branch length estimates, but attributed the difference to inclusion of leaves in weight estimates. These relative differences in estimates of percent utilization are probably unimportant for species such as wax currant; but, for browse species that show greater utilization, these differences become more important to managers.

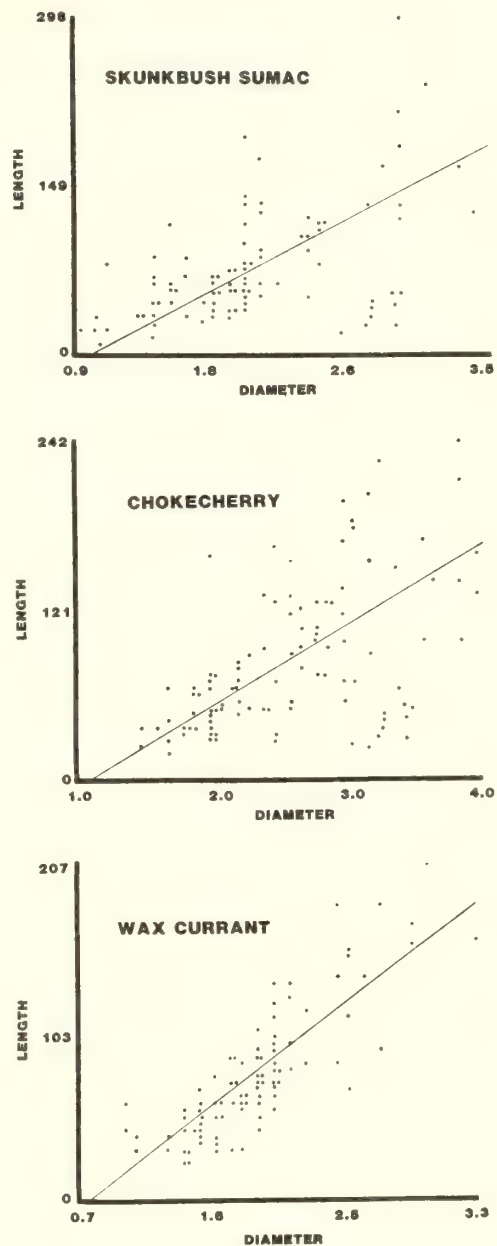


Figure 1.--Relationships of twig length (mm) to twig diameter (mm) for three shrub species in southeastern Montana.

Browsing by animals in this study did not remove large portions of individual twigs. Estimates of the percentages of individual twigs browsed (based on weight estimates) were 26, 37, and 20 percent for skunkbush sumac, chokecherry, and wax currant, respectively. Lyon (1970) suggested big game animals do not browse small percentages of individual twigs, which was contradicted by results of this study. Browsing animals on this study area were pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed jackrabbits (*Lepus townsendii*); livestock grazed portions of the study area.

When designing a study from which to develop a model to predict values, some modifications for

sampling are required. Sampling in this study was pseudorandom in that a few very small and very large stems were deliberately sampled to include the extremes. However, for skunkbush sumac there was an order of magnitude difference between the three largest values and the remainder of the data. Preliminary analysis of the skunkbush sumac twig weight data with the model $Y = a + b_1X + b_2X^2$ resulted in an R^2 of 0.90. However, this regression equation was being driven by the three outlying data points (fig. 2). The resulting negative coefficient (b_1) caused the predicted weights of twigs browsed to be greater than the amount available because the function had a minima at a twig diameter larger than the mean diameter at the browse point. If the model was forced through the origin ($Y = bX^2$), the predicted weight of twigs browsed was negative, again resulting

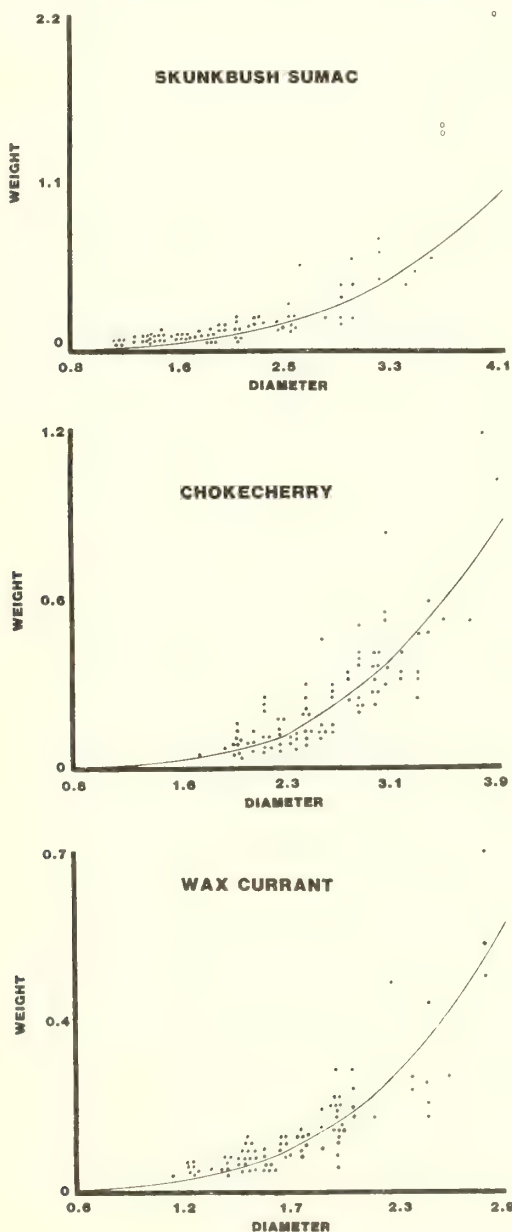


Figure 2.--Relationships of twig weight (g) to twig diameter (mm) for three shrub species in southeastern Montana.

Table 1.--Regression equations to predict length and weight of shrub twigs from twig diameter for three species of shrubs in southeastern Montana

Species	Equation	R^2
Skunkbush sumac	Length = $71.79 (6.1)^1$	0.59
	* (Diameter) - 64.55	
	Weight = $0.007 (0.0004)$	0.80
	* (Diameter) ^{3.58}	
Chokecherry	Length = $58.60 (5.8)$	0.51
	* (Diameter) - 61.53	
	Weight = $0.004 (0.0002)$	0.75
	* (Diameter) ^{4.05}	
Wax currant	Length = $68.75 (5.9)$	0.58
	* (Diameter) - 49.97	
	Weight = $0.011 (0.0005)$	0.81
	* (Diameter) ^{3.69}	

¹The coefficient.

Table 2.--Estimates of percent utilization using length and weight equations for three shrubs species in southeastern Montana

Estimate method	Skunkbush sumac	Chokecherry	Wax currant
Length	11.1	16.9	4.2
Weight	8.4	11.2	2.0

from the larger twig diameters driving the model. Other analyses that included these outliers resulted in the model $Y = aX^b$ having an exponent (b) of 5.73. The R^2 for this model also was 0.90. Examination of the residuals plot indicated the model was not appropriate. These outliers were sucker type growth and therefore were not included in the final analysis. The resulting model (table 1) and residuals plot suggested this model fit the data fairly well.

In the future, a more selective procedure that results in a scattering of data points throughout the range of twig sizes (stratified random sampling) would be more appropriate. Random sampling of twigs concentrates the data points near the middle portions of the distribution. Without the data points at the upper and lower ends of the range (figs. 1, 2) these distributions could result in linear models that have been reported for twig diameter-weight models (Lyon 1970; Peek and others 1971).

Standardized residuals plotted against standardized twig diameters indicated that there were heterogeneous variances in these data. However, nonuniformity of variances will not introduce serious biases to regression models (National Academy of Sciences 1962: 255) provided the data

are scattered throughout the range and there are no outliers. The residual plots indicated that the regression models derived were appropriate for these data. In any case, it is important to examine the residuals to see how well the model fits the data. Plots of residuals also indicate if nonlinear or weighted models should be used and they display possible outliers.

REFERENCES

- Basile, Joseph V.; Hutchings, Selar S. Twig diameter-length-weight relations of bitterbrush. *J. Range Manage.* 19: 34-38; 1966.
- Hull, C., Hadlai; Nie, Norman H. SPSS, Update 7-9; new procedures and facilities for releases. New York, NY: McGraw-Hill 1981. 402 p.
- Jensen, Charles H.; Urness, Philip J. Establishing browse utilization from twig diameters. *J. Range Manage.* 34: 113-116; 1981.
- Lyon, L. Jack. Length- and weight-diameter relations of serviceberry twigs. *J. Wildl. Manage.* 34: 456-460; 1970.
- National Academy of Sciences. Range research: basic problems and techniques. Publ. 890. Washington, DC: National Academy of Sciences, Natural Resource Council; 1962. 341 p.
- Peek, James M.; Krefting, Laurits W.; Tappeiner, John C. Variation in twig diameter-weight relationships in northern Minnesota. *J. Wildl. Manage.* 35: 501-507, 1971.
- Provenza, Frederick D.; Urness, Phillip J. Diameter-length-weight relations for blackbrush (*Coleogyne ramosissima*) branches. *J. Range Manage.* 34: 215-217; 1981.
- Robinson, Barry. SPSS Subprogram NONLINEAR, nonlinear regression. SPSS No. 433. Evanston, IL: Northwestern University; 1984. 28 p.
- Ruyle, G. B.; Bowns, James E.; Schlundt, Al F. Estimating snowberry (*Symphoricarpos oreophilus*) utilization by sheep from twig diameter-weight relations. *J. Range Manage.* 36: 472-474; 1983.
- Telfer, Edmund S. Twig weight-diameter relationships for browse species. *J. Wildl. Manage.* 33: 917-921; 1969.

NATURAL HISTORY OF LITTLE COTTONWOOD CANYON, UTAH:
A FIELD TOUR

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INTRODUCTION

This paper is an invited account of the field trip concluding the August 7-9, 1985, Symposium on Plant/Herbivore Interactions, at Snowbird, UT. It is designed to give a vicarious or in-person visit to the site a biological, geological, and historical perspective.

GEOLOGY

The tour group traveled on the Snowbird aerial tram to its terminus at Mt. Baldy on the southern crest of the Little Cottonwood drainage basin (fig. 1). The tram terminates at a vantage point over 11,000 ft (3,353 m) above sea level. From that point one can see the Uinta Mountains to the east and several of the larger mountain systems of western Utah. As the tram made its ascent, some of the local influences of Pleistocene glaciers

were readily observable. Extensive headlands along the southern wall of the canyon lie above 10,800 ft (3,292 m) elevation. Those areas accumulated enough snow during the Pleistocene to produce large glaciers that shoved their way downslope in both Little Cottonwood and American Fork Canyons. Little Cottonwood's classical U-shape owes its origin to glacial processes. Polished granitic walls and locally conspicuous moraines characterize the lower reaches of the canyon. The glacier flowed from the canyon's mouth and disgorged its ice directly into Lake Bonneville as recently as 15,000 years ago (Curry and James 1982). Bonneville's surface stood as high as 5,200 ft (1,585 m) above sea level some 13,000 yr B.P. Had we stood at the tram's upper station at that time, we would have seen an immense lake (the forerunner of Great Salt Lake) flecked with icebergs and stretching to the western horizon.

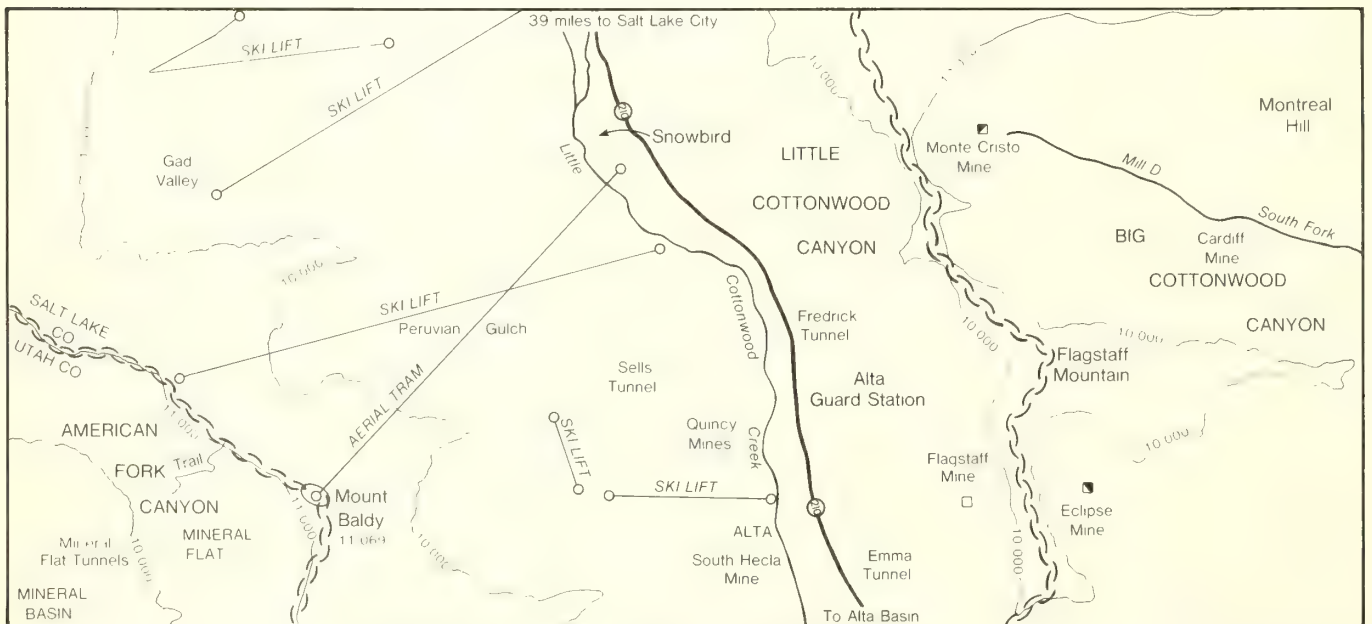


Figure 1.--Portions of Little Cottonwood and American Fork Canyons, Utah, observed on the field trip on August 9, 1985.

Little Cottonwood Canyon has complex structural features. The north wall of the canyon shows an extensive contact zone between intrusive igneous material and deep, overlying beds of sedimentary rocks. Heat and intrusive fissures of igneous material have altered both color and chemistry of sedimentary beds overlying the granitic stock. The basal sedimentary beds of quartzite, tillite, shale, and limestone appear burned and rusty for hundreds of feet above the margins of the stock. Fossils testify that the sedimentary beds in the canyon range in age from Pre-Cambrian to Jurassic. Geologists suggest that the molten stock was thrust into place in late Cretaceous or early Tertiary time (Calkins and Butler 1943). Numerous mine dumps in both Little Cottonwood and American Fork Canyons are visible from the terminus of the tram (fig. 1). They bear witness that most of the local precious metal deposits (silver, lead, copper, gold, and zinc, in order of revenue generated) occurred in fissures in the sedimentary rock just above the igneous-sedimentary contact zone.

BIOTA

Some animals and plants that are often observed in the area shown in fig. 1 are listed in table 1. Many of those species were seen as field trip participants hiked from Mt. Baldy along the trail into Mineral Basin in the American Fork drainage. Despite the fact that prevailing winds at this latitude flow from west to east, the biotas of mountains throughout the Great Basin are derived from mountains to the east. That fact is attributable to the following factors.

- 1) Mountain ranges between the Uintas and the Sierras are progressively younger as one moves from east to west. Thus although the Sierras now have rich biotas at high elevations, geologic evidence suggests that they did not reach elevations high enough to support subalpine and alpine taxa until after about 1.0 million yr B.P. (Axelrod and Ting 1960; Winograd and others 1985). Since all of the Great Basin ranges are older than that, their initial high-elevation colonists would have had to come from elsewhere. The Wasatch is old enough to have been such a source area: high-elevation taxa appear to have been spread westward from the Wasatch by birds or moved overland at times when lowlands were better watered (as in the Pleistocene).
- 2) Climates of the Wasatch are more like those of the desert mountains than those of the Sierras. Organisms adapted to the thermally moderate, high-humidity air masses of coastal California and the western slopes of the Sierras have probably been at a disadvantage as they have dispersed into the more continental and xeric climates of the Great Basin (Harper and others 1978).
- 3) Soils at high elevations in the Sierras are prevaillingly acidic (Major and Taylor 1977), while even igneous outcrops in the Great Basin are often only weakly acidic or are nearly

neutral (Harper and others 1978). Soils of the Wasatch and the sedimentary mountain ranges of eastern Nevada are basic in reaction (Holmgren 1972). Thus plants that are well adapted to the acidic soils of the Sierras tend to perform poorly in the Great Basin because of large differences in soil reaction (Harper and others 1978).

Modern distributional patterns of plants and animals in the Basin and Range Geological Province, and the Wasatch and Sierra Mountains which flank that province, were strongly influenced by environmental conditions that prevailed during the Pleistocene. Studies of biota dependent on the cool, seasonally well-watered habitats of Great Basin mountains show species richness (numbers of species per unit area) patterns reminiscent of patterns observed for oceanic islands. The species numbers tend to increase linearly with area of high-elevation habitat when both variables are expressed as logarithms (Behle 1978; Harper and others 1978). Interestingly, the steepness of the species-area regression lines differ significantly between taxonomic groups that disperse easily between modern islands of cool, moist habitat (birds and many plant species) and groups that now experience great difficulty moving between such habitat islands (many mammals now confined to high elevations). Thus mammals of boreal habitats show very steep regression lines, while birds and many plant groups display more gentle slopes for species-area regressions. Brown (1971, 1978) suggested that the steeper sloped regressions arise when a group has high extinction rates on small patches of habitat that had once been well stocked by species arriving by overland migrations during periods of better moisture relations. Alpine mammal species that appear to be representative of this group of overland dispersers are noted in table 1. As the Pleistocene waned and was followed by more xeric conditions in the Holocene, reinvasion of the small islands of suitable habitat became more difficult or impossible. Recent work has yielded much subfossil evidence that valley floors between modern islands of boreal habitat did support montane and subalpine plants in late Pleistocene times (Wells 1983). Grayson (1982) demonstrated that skeletal remains of several mammals unique to mesic montane or alpine habitats occur on a number of Great Basin ranges that are now too dry for boreal taxa. Those remains date to the late Pleistocene. Thus Brown's (1971) initial hypothesis about local extinctions on small mountain islands in the Great Basin has been supported by subfossil data from caches of biological material assembled by woodrats or prehistoric humans.

On the hike into Mineral Basin, note was taken of the fact that the flower pollinator guild at this site contained numerous dipteran insects. Pollinator guilds at low elevations in Utah are dominated by hymenopteran insects. The divergence of dipteran and hymenopteran insects with elevation seems to be the rule in

Table 1.--Animals and plants commonly seen in the vicinity of Snowbird and the terminus of the Snowbird aerial tram on Mt. Baldy. Common and scientific names (in parentheses) are listed. Mammals of alpine habitats that appear to have dispersed to high Great Basin mountains from the Sierras or the Rocky Mountains when intervening valleys were more mesic during the Pleistocene are marked with an asterisk (from Brown 1971)

Animals	
Birds ¹	Mammals ²
Broad-tailed hummingbird (<u>Selasphorus platycercus</u>)	Deer mouse (<u>Peromyscus maniculatus</u>)
Cassin's finch (<u>Carpodacus cassinii</u>)	*Ermine (<u>Mustela erminea</u>)
Chipping sparrow (<u>Spizella passerina</u>)	*Jumping mouse (<u>Zapus princeps</u>)
Clark's nutcracker (<u>Nucifraga columbiana</u>)	*Long-tailed vole (<u>Microtus longicaudus</u>)
Common flicker (<u>Colaptes auratus</u>)	Mt. goat (<u>Oreamnos americanus</u>)
Dusky flycatcher (<u>Empidonax oberholseri</u>)	Mule deer (<u>Odocoileus hemionus</u>)
Gray-headed junco (<u>Junco caniceps caniceps</u>)	*Pika (<u>Ochotona princeps</u>)
Mountain chickadee (<u>Parus gambeli</u>)	Red squirrel (<u>Tamiasciurus hudsonicus</u>)
Vesper sparrow (<u>Pooecetes gramineus</u>)	Snowshoe hare (<u>Lepus americanus</u>)
Water pipit (<u>Anthus spinoletta</u>)	*Uinta chipmunk (<u>Eutamias umbrinus</u>)
Yellow-rumped warbler (<u>Dendroica coronata</u>)	Uinta ground squirrel (<u>Spermophilus armatus</u>)
	*Yellow-bellied marmot (<u>Marmota flaviventris</u>)
Plants ³	
Trees	Shrubs
Englemann spruce (<u>Picea engelmannii</u>)	Alpine prickly currant (<u>Ribes montigenum</u>)
Limber pine (<u>Pinus flexilis</u>)	Blue willow (<u>Salix drummondiana</u>)
Mt. alder (<u>Alnus incana</u>)	Mt. lover (<u>Pachistima myrsinites</u>)
Quaking aspen (<u>Populus tremuloides</u>)	Mt. snowberry (<u>Symphoricarpos oreophilus</u>)
Subalpine fir (<u>Abies lasiocarpa</u>)	Oregon grape (<u>Berberis repens</u>)
	Red-berried elder (<u>Sambucus racemosa</u>)
Grasslike Plants	Forbs
Alpine bluegrass (<u>Poa alpina</u>)	Arizona bluebell (<u>Mertensia arizonica</u>)
Drummond rush (<u>Juncus drummondii</u>)	Brandegge onion (<u>Allium brandegei</u>)
Letterman needlegrass (<u>Stipa lettermanii</u>)	Cloverhead horsemint (<u>Monardella odoratissima</u>)
Mt. brome (<u>Bromus carinatus</u>)	Colorado columbine (<u>Aquilegia caerulea</u>)
Ross sedge (<u>Carex rossii</u>)	Dunecap larkspur (<u>Delphinium occidentale</u>)
Scribner wheatgrass (<u>Agropyron scribneri</u>)	Engelmann aster (<u>Aster engelmannii</u>)
Slender wheatgrass (<u>A. trachycaulum</u>)	False hellebore (<u>Veratrum californicum</u>)
Spike trisetum (<u>Trisetum spicatum</u>)	Fireweed (<u>Epilobium angustifolium</u>)
Tufted hairgrass (<u>Deschampsia cespitosa</u>)	Leafy Jacob's ladder (<u>Polemonium foliosissimum</u>)
Western sedge (<u>C. occidentalis</u>)	Marsh marigold (<u>Caltha leptosepala</u>)
	Monkshood (<u>Aconitum columbianum</u>)
	Parry arnica (<u>Arnica parryi</u>)
	Showy goldeneye (<u>Viguiera multiflora</u>)

¹ Bird names follow Behle and Perry (1975).

² Mammal nomenclature is after Brown (1971) and Grayson (1982).

³ Plant names are from Arnow and others (1980).

mountain-valley systems throughout the earth (Warren and others, in press). Collins and others (1983) suggested that a statistically significant decline in sympetalous, yellow, tubular flowers with increasing elevation in Utah and a simultaneous rise in abundance of polypetalous, white, saucer-shaped flowers are related to strong differences in the foraging preferences of dipteran and hymenopteran pollinating insects. The differential success of dipterans and hymenopterans at high elevations seems related to basic differences

in their life history patterns and behavior. Hymenopterans universally make chambers in which they deposit eggs and food for larvae, which emerge from eggs after the compartment is sealed. The food provided consists of pollen mixed with secretions from the adults. In contrast, dipterans build no nest structures and provide no parental care. Hymenopterans also thermoregulate (increase thoracic temperature) to permit flight in the colder environments of high elevations. Thermoregulation is made possible by frictional heat resulting from

rapid wing movement without flight. That process uses considerable energy, since thoracic temperatures must be elevated to 18-20°C before flight is possible. Dipterans raise body temperature to levels that permit flight by passive basking in the sun. Thus dipterans have at least two energetic advantages over hymenopterans at high elevations (Arroyo and others 1981; Warren and others, in press).

The mountain goat (table 1) represents a recent introduction to the higher elevation alpine habitats of the Wasatch Mountains. Herds are thriving on both Mt. Timpanogos to the south of the area shown in fig. 1 and along the divide between Little and Big Cottonwood Canyons. Wandering animals are occasionally seen along the divide between Little Cottonwood and American Fork drainages.

REFERENCES

- Arnow, L.; Albee, B.; Wyckoff, A. Flora of the central Wasatch Front, Utah. Salt Lake City, Utah: University of Utah Printing Service; 1980: 663 p.
- Arroyo, M. T. K.; Primack, R.; Armesto, J. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany*. 69: 82-97; 1981.
- Axelrod, D. I.; Ting, W. S. Late Pliocene floras east of the Sierra Nevada. University of California Publications in Geological Sciences. 39: 1-118; 1960.
- Behle, W. H. Avian biogeography of the Great Basin and Intermountain Region. *Great Basin Naturalist Memoirs*. 2: 55-76; 1978.
- Behle, W. H.: Perry, M. L. Utah birds - guide, check-list and occurrence charts. Salt Lake City, Utah: Paragon Press; 1975: 144 p.
- Brown, J. H. Mammals on mountain tops: nonequilibrium insular biogeography. *American Naturalist*. 105: 467-478; 1971.
- Brown, J. H. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs*. 2: 209-227; 1978.
- Calkins, F. C.; Butler, B. S. Geology and ore deposits of the Cottonwood-American Fork area, Utah. Professional Paper 201. Washington, D.C.: U.S. Department of the Interior, Geological Survey; 1943: 1-152.
- Collins, P. D.; Harper, K. T.; Pendleton, B. K. Comparative life history and floral characteristics of desert and mountain floras in Utah. *Great Basin Naturalist*. 43: 385-393; 1983.
- Curry, D. R.; James, S. R. Paleoenvironments of the northeastern Great Basin and northeastern basin rim region: a review of geological and biological evidence. In: Madsen, D. B.; O'Connell, J. F., eds. *Man and environment in the Great Basin*. Paper No. 2. Washington, D.C.: Society for American Archaeology; 1982: 27-52.
- Grayson, D. Toward a history of Great Basin mammals during the past 15,000 years. In: Madsen, D. B.; O'Connell, J. F., eds. *Man and environment in the Great Basin*. Paper No. 2. Washington, D.C.: Society for American Archaeology; 1982: 82-101.
- Harper, K. T.; Freeman, D. C.; Ostler, W. K.; Klikoff, L. G. The flora of Great Basin mountain ranges; diversity, sources, and dispersal ecology. *Great Basin Naturalist Memoirs*. 2: 81-103; 1978.
- Holmgren, N. H. Plant geography of the Intermountain region. In: Cronquist, A.; Holmgren, A. H.; Holmgren, N. H.; Reveal, J. L., eds. *Intermountain flora: vascular plants of the Intermountain West, U.S.A.* New York: Hafner; 1972: 77-161.
- Major, J.; Taylor, D. W. Alpine. In: Barbour, M. G.; Major, J., eds. *Terrestrial vegetation of California*. New York: John Wiley and Sons; 1977: 601-675.
- Warren, S. D.; Harper, K. T.; Booth, G. M. Elevational distribution of insect pollinators. *Great Basin Naturalist* 47 (in press); 1987.
- Wells, P. V. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecological Monographs*. 53: 341-382; 1983.
- Winograd, I., J.; Szabo, B. J.; Coplen, T. B.; Riggs, A. C.; Kolesar, P. T. Two-million-year record of deuterium depletion in Great Basin ground waters. *Science*. 227: 519-522; 1985.

Provenza, Frederick D.; Flinders, Jerran T.; McArthur, E. Durant, compilers. Proceedings--symposium on plant-herbivore interactions; 1985 August 7-9; Snowbird, UT. General Technical Report INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1987. 179 p.

Fourth in a series of proceedings of symposia on wildland shrubs, this publication brings together current knowledge of interactions between plants and herbivores. Topics addressed by the 31 papers include plant chemistry, palatability, nutrition and physiology, herbivore foraging behavior, and plant response to browsing.

KEYWORDS: wildland shrubs, photosensitization, cattle abortion, chemistry, palatability, nutrition, foraging behavior, browsing response, physiology

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Forest Service

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Fire Ecology of Western Montana Forest Habitat Types

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RESEARCH SUMMARY

This report summarizes available information on fire as an ecological factor for forest habitat types in western Montana. The forest habitat types are assigned to Fire Groups based primarily on fire's role in forest succession. For each Fire Group, information is presented on (1) the relationships of major tree species to fire, (2) fire effects on undergrowth, (3) forest fuels, (4) the natural role of fire, (5) fire and forest succession, and (6) fire management considerations.

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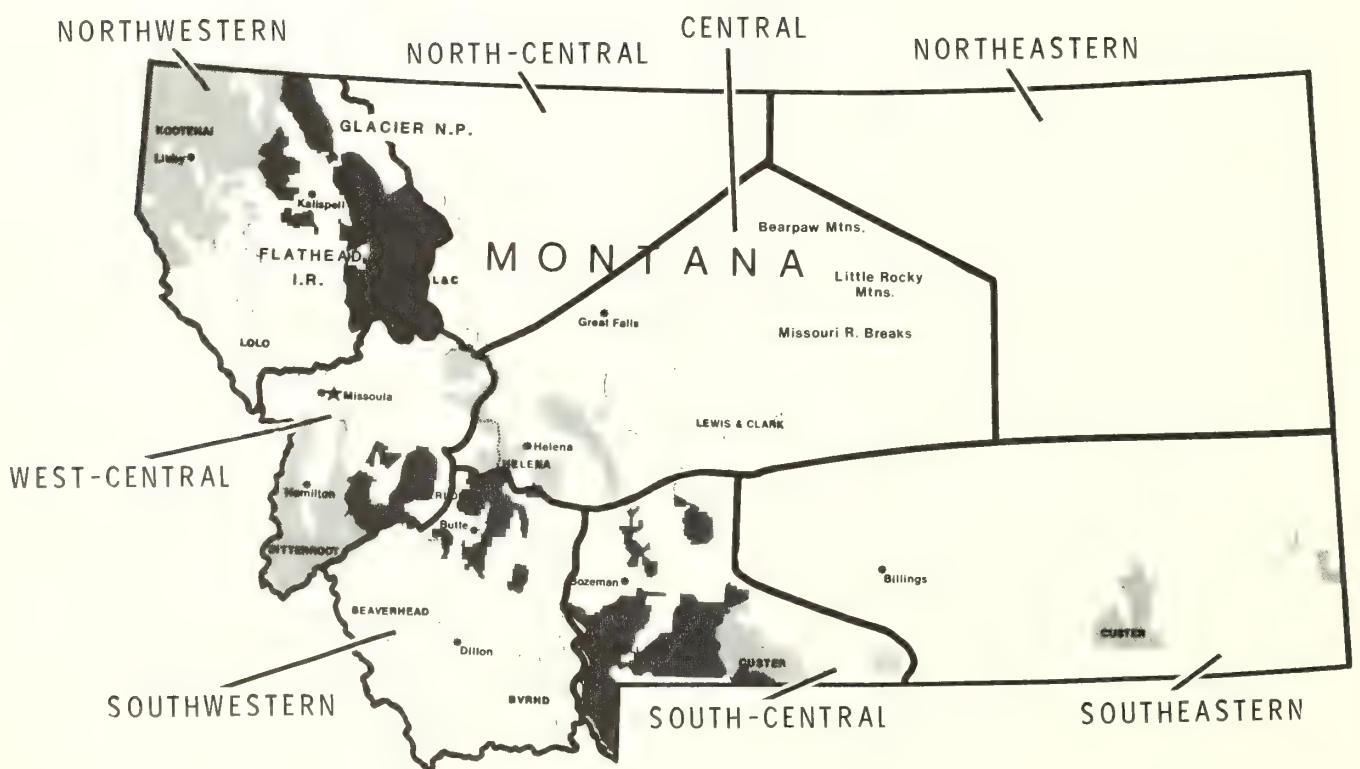


Figure 1—Forest regions of Montana (source: Arno 1979).

Fire Ecology of Western Montana Forest Habitat Types

William C. Fischer
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INTRODUCTION

This report summarizes available fire ecology and management information that applies to forest habitat types west of the Continental Divide in Montana—specifically, on the Bitterroot, Flathead, Kootenai, and Lolo National Forests; the western portions of the Deerlodge and Helena National Forests and Glacier National Park; the Flathead Indian Reservation; and on adjoining State and private timberlands. The primary purpose of this report is to help forest managers understand the role of fire in western Montana forests, especially the role of fire in forest tree succession.

Habitat types are assigned to 10 “Fire Groups” based on the response of the tree species to fire and the roles these tree species take during successional stages. The exception is Fire Group Zero, which is a description of miscellaneous vegetation types. Because Fire Groups One and Three only occur east of the Continental Divide in Montana, they are not discussed in this report (see Fischer and Clayton 1983).

The Fire Groups defined in this report include a number of borderline cases. Differences in fire behavior and in successional patterns often depend on small local changes in fuel, temperature, moisture, sunlight, topography, and seed availability. Thus, it would be possible for stands that key to the same habitat type to fall into different Fire Groups. Assignment of habitat types to more than one Fire Group is kept to a minimum in this report. A certain reliance is placed on the judgment of the land manager in evaluating the local conditions of any particular site. The groups defined in this report are intended as a general guide, not a definitive treatment.

Format

This report is patterned after “Fire Ecology of Montana Forest Habitat Types East of the Continental Divide” (Fischer and Clayton 1983) and essentially updates and expands the scope of a previous report, “Fire Ecology of the Lolo National Forest” (Davis and others 1980), which is no longer available.

The major topics presented in this report are:

Relationship of Major Tree Species to Fire—This section contains a discussion of each principal tree species in western Montana forests with regard to its resistance or susceptibility to fire and its role as a successional component of forest communities. Particular attention is given

to special adaptations to fire, such as corky bark, serotinous cones, or seeds that require mineral soil for germination.

Undergrowth Response to Fire—This is a brief summary of the effect of fire on the response of important understory grass, forb, and shrub species. Particular attention is given to fire-adaptive traits or survival strategies that determine whether fire generally increases or decreases species cover in the immediate postfire period.

Wildlife Response to Fire—This section contains brief summaries of the general effects of fire on common western Montana mammals, reptiles, amphibians, and birds. Fire response of wildlife is largely inferred from expected changes in habitat as a result of fire.

Fire Use Considerations—This briefly summarizes cautions that apply to the use of fire for resource management purposes. Emphasis is on effective use of fire, site protection, minimizing damage to residual stand, and wildlife habitat protection.

Habitat Types and Phase, ADP Codes, and Forest Region—The Fire Groups are defined with reference to “Forest Habitat Types of Montana” (Pfister and others 1977). A complete list of the habitat types west of the Continental Divide in Montana is included as appendix A.

Habitat types are designated in the standard format of “series/type-phase,” in which “series” designates the potential climax dominant tree, “type” designates a definitive undergrowth species, and “phase” provides a further subdivision where needed. The “ADP codes” are the automatic data processing codes for National Forest System use in the Forest Service Northern Region.

The forest region designation refers to those described for Montana by Arno (1979) as illustrated in figure 1.

Vegetation—We describe the characteristic overstory and understory vegetation for each Group. Climax and seral species are identified. A complete distribution of tree species showing their successional status is included as appendix B.

Forest Fuels—For each Fire Group, we discuss the kind and amount of dead, woody material likely to be found on the forest floor. The discussion is based on fuel inventory data (Brown 1974) from two sources. The prime source is a photo series for appraising natural fuels in wild stands on Montana National Forests (Fischer 1981a, 1981b, 1981c). The other source is a summary of downed woody fuel on National Forests in the Northern Rockies (Brown

and See 1981). Summary fuel information pertaining to all Fire Groups is presented in a separate section preceding the Fire Group discussions.

It is important to remember that these discussions are about dead, woody material on the forest floor. Live fuel and standing dead fuel are treated casually, if at all, because fuel data on this material were not collected as part of the inventories mentioned above.

Cover type names used in this section were suggested by the Society of American Foresters (Eyre 1980).

Role of Fire—Information on the important trees and forest fuel characteristics is integrated with the results of fire history studies to describe the historical (presettlement period, generally prior to 1900) role of fire in shaping the vegetative composition of a particular Fire Group. This section is mainly a literature review covering succession and fire within the appropriate habitat types.

For this report, three levels of fire severity are recognized: low or cool, moderate, and high or severe. A **low-severity** or **cool fire** is one that has minimal impact on the site. It burns in surface fuels consuming only the litter, herbaceous fuels, and foliage and small twigs on woody undergrowth. Little heat travels downward through the duff. A **moderate fire** burns in surface fuels but may also involve a tree understory. It consumes litter, upper duff, understory plants, and foliage on understory trees. Individuals and groups of overstory trees may torch out if fuel ladders exist. A **high-severity** or **severe fire** is one that burns through the overstory and consumes large woody surface fuels or removes the entire duff layer over much of the area. Heat from the fire impacts the upper soil layer and often consumes the incorporated soil organic matter.

Forest Succession—The generalized succession diagram and associated text represents a simplified, synthetic overview of fire's role in succession for each Fire Group.

The diagram for each Fire Group represents a visual summary of the effects that fires of varying severity can have on the habitat types that make up the group. Secondary succession begins with the shrub/herb stage, but the diagram can be used from any stage of stand development. Numerous facts that may influence the vegetation on the landscape have been neglected to emphasize the potential influences of fire and fire suppression.

Successional pathway flow charts represent a synthesis of confirmed knowledge and unconfirmed speculation that forms a complex series of hypotheses concerning the many possible influences fire may have on the vegetation of the Fire Groups. The flow charts follow the method suggested by Kessell and Fischer (1981).

How trees respond to fire often depends on their size. Tree size classes used in our flow charts are defined by the Society of American Foresters (1958). **Saplings** are trees 2 to 4 inches in diameter at breast height (d.b.h.). **Small poles** are trees 4 to 8 inches d.b.h. **Large poles** are trees 8 to 12 inches d.b.h.

The conifer species names are symbolized to simplify the diagrams and flow charts. The symbols are defined as follows:

Abies grandis, grand fir (ABGR)

Abies lasiocarpa, subalpine fir (ABLA)

Juniperus scopulorum, Rocky Mountain juniper (JUSC)

Larix lyallii, subalpine larch (LALY)

Larix occidentalis, western larch (LAOC)

Picea engelmannii, Engelmann spruce (PICEA)

Pinus albicaulis, whitebark pine (PIAL)

Pinus contorta, lodgepole pine (PICO)

Pinus monticola, western white pine (PIMO)

Pinus ponderosa, ponderosa pine (PIPO)

Pseudotsuga menziesii, Douglas-fir (PSME)

Thuja plicata, western redcedar (THPL)

Tsuga heterophylla, western hemlock (TSHE)

Tsuga mertensiana, mountain hemlock (TSME)

Fire Management Considerations—This section suggests how the preceding information can be used to develop fire management plans that support land and resource management objectives. The discussion is intended to be suggestive, not dogmatic. Each manager is in a much better position than are the authors to relate the information in this report to a particular management situation.

The Fire Groups

The forest habitat types of Montana have been assembled into 12 Fire Groups (table 1) that are defined as follows:

Fire Group Zero: A miscellaneous, heterogeneous collection of special habitats. In western Montana forests these sites exist as scree, forested rock, wet meadow, mountain grassland, aspen grove, and alder glade.

Fire Group One: Dry limber pine habitat types. These occur almost exclusively east of the Continental Divide in Montana.

Fire Group Two: Warm, dry ponderosa pine habitat types. This group consists of both open ponderosa pine stands with a predominantly grass undergrowth and dense mixed-aged stands of ponderosa pine. These sites may exist as fire-maintained grasslands and do not support Douglas-fir, except as "accidental" individuals.

Fire Group Three: Warm, moist ponderosa pine habitat types. These sites occur exclusively east of the Continental Divide in Montana. These sites are often occupied by stagnant, overgrown thickets of ponderosa pine saplings.

Fire Group Four: Warm, dry Douglas-fir habitat types. Under "natural" conditions, these sites support fire-maintained ponderosa pine stands. In the absence of fire, Douglas-fir regenerates beneath the pine and eventually dominates the overstory.

Fire Group Five: Cool, dry Douglas-fir habitat types. Douglas-fir is often the only conifer present on these sites. In the absence of fire, a dense Douglas-fir sapling understory may develop.

Fire Group Six: Moist Douglas-fir habitat types. Douglas-fir often dominates all stages of succession on these sites, even when subjected to periodic fire.

Fire Group Seven: Cool habitat types usually dominated by lodgepole pine. This group includes stands in which fire maintains lodgepole pine as a dominant seral species as well as those stands in which lodgepole is a persistent dominant.

Table 1—Summary of Montana forest habitat type Fire Groups (see appendix C for formal listing of habitat type Fire Groups)

Habitat type ¹	Forest region ²	Habitat type ¹	Forest region ²	Habitat type ¹	Forest region ²
FIRE GROUP ONE		FIRE GROUP SIX		FIRE GROUP NINE	
PIFL/AGSP	NC,C,SW,SC	PSME/PHMA-PHMA	NW,WC,C,SW,SC	PICEA/EQAR	NW,NC,C,SW,SC
PIFL/FEID-FEID	NC,C,SW,SC	PSME/VICA*	C	PICEA/CLUN-VACA	NW
PIFL/FEID-FESC	NC,C	PSME/VAGL-VAGL	NW,WC,C,SW,SC	PICEA/CLUN-CLUN	NW
PIFL/JUCO	NC,C,SW,SC	PSME/VAGL-ARUV	NW,WC,C	PICEA/GATR	WC,C,SW,SC
FIRE GROUP TWO		PSME/VAGL-XETE	NW,WC,C	ABLA/OPHO	NW
PIPO/AND	SE	PSME/LIBO-SYAL	NW,WC,C	ABLA/CLUN-CLUN	NW,WC,NC
PIPO/AGSP +	NW,WC,C,SE	PSME/LIBO-ARUV*	C	ABLA/CLUN-ARNU	NW,WC,NC
PIPO/FEID-FEID	WC,C,SE	PSME/LIBO-CARU +	NW,WC,C,SW	ABLA/CLUN-VACA	NW,WC
PIPO/FEID-FESC +	NE,WC,C	PSME/LIBO-VAGL	WC,C	ABLA/CLUN-XETE	NW,WC,NC
PIPO/PUTR-AGSP	WC,C	PSME/SYAL-CARU	NW,WC,C,SW,SC	ABLA/CLUN-MEFE	NW,WC,NC
PIPO/PUTR-FEID	NW,WC,C	PSME/SYAL-SYAL	NW,WC,NC,C,SW,SC	ABLA/GATR	WC,NC,C,SC
PIPO/SYAL-SYAL	NW,WC,C,SE	PSME/AMAL*	C	ABLA/CACA-CACA	WC,C,SW,SC
PIPO/SYOC*	C	PSME/CARU-ARUV	NW,WC,C	ABLA/CACA-GATR	WC,C,SW
PIPO/ARUV*	C	PSME/CARU-CARU	NW,WC,NC,C,SW,SC	ABLA/LIBO*	C
PIPO/JUHO*	C	PSME/VACA	NW,WC	ABLA/LIBO-LIBO	NW,WC,NC,C,SW,SC
PIPO/JUSC**	C	PSME/JUCO	NC,C,SW	ABLA/LIBO-XETE	NW,WC
FIRE GROUP THREE		FIRE GROUP SEVEN		ABLA/MEFE	NW,WC,NC,SW,SC
PIPO/SYAL-BERE	C,SE	PSME/JUCO	NC,C,SW	TSME/MEFE	NW,WC
PIPO/BERE*	C	PSME/VACA	NW,WC,NC,C	ABLA/ALSI	WC,NC,SW,SC
PIPO/AMAL*	C	PSME/COCA-LIBO*	C	FIRE GROUP TEN	
PIPO/PRVI-PRVI	SE	PSME/COCA-VAMY*	C	PICEA/SEST-PICEA	C
PIPO/PRVI-SHCA	SE	PICEA/VACA	NW,NC	PICEA/JUCO*	C
FIRE GROUP FOUR		PICEA/LIBO	WC,C,SC,SW	PICEA/RIMO*	SW,SC
PSME/AGSP	NW,WC,C,SW,SC	ABLA/VACA	NW,WC,C,SW	ABLA-PIAL/VASC	WC,NC,C,SW,SC
PSME/FESC	NW,WC,C	ABLA/CACA-VACA	NW,WC,C,SW	ABLA/LUHI-VASC	NW,WC,NC,SW
PSME/PHMA-CARU	NW,WC	ABLA/LIBO-VASC	NW,WC,NC,C,SC,SW	ABLA/LUHI-MEFE	NW,WC,C
PSME/SYAL-AGSP	NW,WC,C	ABLA/XETE-VASC	NW,WC,NC,SW	ABLA/JUCO*	C
PSME/SYOC-CHVI*	C	ABLA/VAGL	WC,C,SC,SW	TSME/LUHI-VASC	NW
PSME/SYOC-SHCA*	C	ABLA/VASC-CARU	C,SC,SW	TSME/LUHI-MEFE	NW
PSME/CARU-AGSP	NW,WC	ABLA/VASC-VASC	NW,WC,C,SC,SW	PIAL-ABLA h.t.'s	NW,WC,NC,C,SW,SC
PSME/CARU-PIPO	NW,WC,C	ABLA/CAGE-CAGE	NC,SW	LALY-ABLA h.t.'s	NW,WC,SW
PSME/SPBE	NW,WC,C,NC	PICO/PUTR	SC	PIAL h.t.'s	WC,C,SW,SC
PSME/ARUV +	C,SC	PICO/VACA	WC,NC,C,SW	FIRE GROUP ELEVEN	
PSME/BERE-ARUV*	C	PICO/LIBO +	NW,WC,C,SC,SW	ABGR/XETE	NW,WC
PSME/BERE-BERE*	C	PICO/VASC	NW,WC,C,SC,SW	ABGR/CLUN-CLUN	NW,WC
PSME/JUSC**	C	PICO/CARU	C,SC,SW	ABGR/CLUN-ARNU	NW,WC
PSME/MUCU**	C	PICO/JUCO	C	ABGR/CLUN-XETE	NW
FIRE GROUP FIVE		FIRE GROUP EIGHT		ABGR/LIBO-LIBO	NW,WC
PSME/FEID	NW,WC,SW,SC	PICEA/LIBO*	C	ABGR/LIBO-XETE	NW
PSME/CARU-AGSP	C	PICEA/PHMA	SC	THPL/CLUN-CLUN	NW,WC
PSME/CAGE	WC,C,SC,SW	PICEA/SMST	WC,C,SW,SC	THPL/CLUN-ARNU	NW,WC
PSME/ARCO	C,SW	ABLA/XETE-VAGL	NW,WC,NC,SW	THPL/CLUN-MEFE	NW,WC
PSME/SYOR	SW	TSME/XETE	NW	THPL/OPHO	NW
PICEA/SEST-PSME	NC,C,SW	ABLA/VASC-THOC	C,SW	TSHE/CLUN-CLUN	NW
		ABLA/CARU	NC,C,SW,SC	TSHE/CLUN-ARNU	NW
		ABLA/CLPS	NC,C,SW,SC		
		ABLA/ARCO	NC,C,SW		
		ABLA/CAGE-PSME	C,SW,SC		

¹Habitat types are as described by Pfister and others (1977) except those designated as follows:

*habitat types of Bearpaw and Little Rocky Mountains (Roberts 1980)

**habitat types of Missouri River Breaks (Roberts and Sibbersen 1979)

+ common to both Pfister and others (1977) and Roberts (1980).

²Forest regions are as described by Arno (1979).

Fire Group Eight: Dry, lower subalpine habitat types. This is a collection of habitat types in the spruce and subalpine fir series that usually support mixed stands of Douglas-fir and lodgepole pine.

Fire Group Nine: Moist, lower subalpine habitat types. Fires are infrequent but severe in these types, and the effects of fire are long lasting. Spruce is usually a major component of seral stands.

Fire Group Ten: Cold, moist upper subalpine and timberline habitat types. This is a collection of high-elevation habitats in which fires are infrequent. Fires are often small in areal extent because of normally sparse fuels. Severe fires have long-term effects. Subalpine fir, spruce, whitebark pine, and subalpine larch are the predominant conifers.

Fire Group Eleven: Moist grand fir, western redcedar, and western hemlock habitat types. These are generally moist habitats in which fires are infrequent but often severe. In Montana they occur exclusively west of the Continental Divide.

Because Fire Groups One and Three do not occur in western Montana, they will not be discussed in this report. A detailed listing of the Fire Groups by habitat type is provided in appendix C.

Nomenclature

Common names of trees and undergrowth plants are used throughout the text of the report. Scientific plant names that correspond to the common names used in the text are listed in appendix D. Common and scientific names follow the "Checklist of United States Trees (Native and Naturalized)" by Little (1979) and the "National Handbook of Plant Names" (USDA-SCS 1981).

Exceptions may occur in habitat type names, which follow the sources listed in table 1.

RELATIONSHIPS OF MAJOR TREE SPECIES TO FIRE

Wildfire plays a major role in forest succession throughout the Northern Rocky Mountains, including forests in western Montana. Lodgepole pine, for example, owes its present widespread occurrence to past fire. Without fire, Douglas-fir would dominate areas where ponderosa pine now occurs but is not climax. Similarly, periodic fire allows western larch and western white pine to persist on many sites where they are not climax. Fire also favors Engelmann spruce at the expense of subalpine fir (Wellner 1970).

Table 2 summarizes the relative fire resistance of the principal conifers in western Montana forests. Minore (1979) provides a more complete review of comparative autecological characteristics of Northwestern tree species.

Ponderosa Pine (*Pinus ponderosa*)

Ponderosa pine has many fire-resistant characteristics. Seedlings and saplings are often able to withstand fire. Seedlings and saplings can maintain themselves on sites with fire intervals as short as 6 years if fire severity is low. Development of insulative bark and the tendency for meristems to be shielded by enclosing needles and thick bud scales contribute to the temperature resistance of pole-sized and larger trees.

Propagation of fire into the crown of pole-sized and larger trees growing in relatively open stands (dry sites) is unusual. First, the tendency of ponderosa pine to self-prune lower branches keeps the foliage separated from

Table 2—Relative fire resistance of the principal conifers occurring west of the Continental Divide in Montana (source: Flint 1925)

Species	Thickness of bark of old trees	Root habit	Resin in old bark	Tolerance		Relative inflammability of foliage	Lichen growth	Degree of fire resistance
				Branch habit	Stand habit			
Western larch	Very thick	Deep	Very little	High and very open	Open	Low	Medium heavy	Most resistant
Ponderosa pine	Very thick	Deep	Abundant	Moderately high and open	Open	Medium	Medium to light	Very resistant
Douglas-fir	Very thick	Deep	Moderate	Moderately low and dense	Moderate to dense	High	Heavy medium	Very resistant
Grand fir	Thick	Shallow	Very little	Low and dense	Dense	High	Heavy	Medium
Lodgepole pine	Very thin	Deep	Abundant	Moderately high and open	Open	Medium	Light	Medium
Western white pine	Medium	Medium	Abundant	High and dense	Dense	Medium	Heavy	Medium
Western redcedar	Thin	Shallow	Very little	Moderately low and dense	Dense	High	Heavy	Medium
Engelmann spruce	Thin	Shallow	Moderate	Low and dense	Dense	Medium	Heavy	Low
Mountain hemlock	Medium	Medium	Very little	Low dense	Dense	High	Medium to heavy	Low
Western hemlock	Medium	Shallow	Very little	Low dense	Dense	High	Heavy	Low
Subalpine fir	Very thin	Shallow	Moderate	Very low and dense	Moderate to dense	High	Medium to heavy	Very low

burning surface fuels. Second, the open, loosely arranged foliage does not lend itself to combustion or the propagation of flames. Third, the thick bark is relatively unburnable and does not easily carry fire up the bole or support residual burning. Resin accumulations, however, can make the bark more flammable.

On moist ponderosa pine sites, Douglas-fir or grand fir often form dense understories, which may act as fuel ladders that can carry surface fires to the overstory. Consequently, crown fires are more frequent on moist sites than they are on dry sites. Understory ponderosa pine may also be more susceptible to fire damage because crowded conditions can result in slower diameter growth. Such trees do not develop their protective layer of insulative bark as early as do faster growing trees. They remain vulnerable to cambium damage from ground fires longer than their counterparts in open stands. The thick, overcrowded foliage of young stands or thickets also negates the fire-resisting characteristic of open, discontinuous crown foliage commonly found in this species.

Ponderosa pine seedling establishment is favored when fire removes the forest floor litter and grass and exposes mineral soil. Fire resistance of the open, parklike stands is enhanced by generally light fuel quantities. Heavy accumulations of litter at the base of trunks increase the intensity and duration of fire, often resulting in a fire scar or "cat face." Flammable resin deposits around wounds can make an individual tree susceptible to fire damage and can enlarge existing fire scars.

Because ponderosa pine is among the most fire-resistant trees growing in Montana, it has a competitive advantage over most other species when mixed stands burn.

Rocky Mountain Juniper (*Juniperus scopulorum*)

Young juniper trees are easily killed by fire primarily because of their small size, thin bark, and compact crown. Fire has long been recognized as a means to control this species because juniper does not resprout. Often young trees are killed just by scorching the crown and stem.

As juniper ages, the bark thickens and the crown develops a bushy, open form. A hot fire can kill or severely damage such a tree, but the same tree may survive a cool fire. Low, spreading branches can provide a route for fire to enter the crown, thereby increasing the potential for damage. Often large junipers have survived a number of fires (four to six).

The different effects of fire on young and old juniper trees are largely a function of the site. The species commonly occupies dry environments that support limited undergrowth. When surface fuels are sparse, fire damage is minimal.

Douglas-fir (*Pseudotsuga menziesii*)

Mature Douglas-fir is a relatively fire-resistant tree. Saplings, however, are vulnerable to surface fires because of their thin, photosynthetically active bark, resin blisters, closely spaced flammable needles, and thin twigs and bud

scales. The moderately low and dense branching habit of saplings enables surface fires to be carried into the crown layer. Older trees develop a relatively unburnable, thick layer of insulative corky bark that provides protection against cool to moderately severe fires. Fire-resistant bark takes about 40 years to develop on moist (favorable) sites. This protection is often offset by a tendency to have branches the length of the bole. The development in the lower trunk of "gum cracks," which streak the bark with resin, can provide a mechanism for serious fire injury.

Douglas-fir often occurs in open stands, but it also grows in dense stands with continuous fuels underneath. Dense sapling thickets can form an almost continuous layer of flammable foliage about 10 to 26 ft (3 to 8 m) above ground that will support wind-driven crown fires. Even small thickets of saplings provide a route by which surface fires can reach the crowns of mature trees.

As with ponderosa pine, heavy fuel accumulations at the base of the tree increase the probability of fire injury. Also, resin deposits often contribute to the enlargement of old fire scars during subsequent fires.

Engelmann Spruce (*Picea engelmannii*)

Engelmann spruce, including hybrids with white spruce (*Picea glauca*) (Habeck and Weaver 1969), is easily killed by fire. The dead, dry, flammable lower limbs, low-growing canopy, thin bark, and lichen growth in the branches contribute to the species' vulnerability. The shallow root system is readily subject to injury from fire burning through the duff. Large old spruce may occasionally survive one or more light fires, but deep accumulations of resinous needle litter around their bases usually make them particularly susceptible to fire damage. Survivors are often subjected to successful attack by wood-destroying fungi that easily enter through fire scars. The high susceptibility of spruce to fire damage is mitigated in part by the generally cool and moist sites where it grows.

Spruce is not an aggressive pioneer. It is a moderate seeder, but seed viability is rated good and the vitality persistent (Alexander and Sheppard 1984). Seedlings can survive on a wide variety of seedbeds. Initial establishment and early growth of seedlings may be slow, but is usually good when encouraged by shade and abundant moisture. Spruce seedlings will occur as members of a fire-initiated stand with lodgepole pine. Spruce's shade tolerance allows it to establish and grow beneath a lodgepole pine canopy. On sites where it is the indicated climax species, spruce will eventually dominate the stand, but it takes a long period without any fire before this can occur.

Restocking will occur more quickly if some spruce trees survive within the burn than if regeneration is dependent on seed from trees at the fire edge. Pockets of spruce regeneration often become established around such surviving seed trees up to a distance of 300 ft (90 m), the effective seeding distance for spruce. Successful regeneration diminishes 100 to 150 years after establishment due to insufficient sunlight at ground level and to accumulating duff. At this point, the more tolerant subalpine fir begins to dominate in the understory.

Western Larch (*Larix occidentalis*)

Western larch is the most fire-resistant conifer in the Northern Rocky Mountains. It possesses an insulating bark that can, in mature trees, range from 3 to 6 inches (7 to 15 cm) thick. The fire resistance of western larch is enhanced by its tendency to self-prune lower branches and its tolerance of defoliation. Western larch is a deciduous conifer and replaces its needles annually. Defoliation by fire is less traumatic for larch than for conifers that normally replace their needles at 2- or 3-year intervals.

Western larch can become established rapidly on mineral soil exposed by fire. Its lightweight seeds can be blown from considerable distances to potential germination sites. A highly intolerant species, western larch requires full or near-full sun for best development. Lodgepole pine and larch are both potential seral dominants on many sites. Western larch is a better competitor where there is higher soil moisture.

Western larch is long lived. Old fire-scarred tree stumps in the Seeley Lake area of western Montana indicate ages in excess of 900 years at the time of cutting. Such longevity helps maintain larch as a stand component and potential seed source for many years.

Lodgepole Pine (*Pinus contorta*)

Individual mature lodgepole pine trees are moderately resistant to surface fires. Lodgepole's thin bark makes it susceptible to death from cambium heating. However, lodgepole pine is alone in its ability to perpetuate itself on a site despite fire. Indeed, on most sites where lodgepole grows, fire is necessary for the species' continued dominance.

Lodgepole pine's key fire survival attribute is cone serotiny. Although there are exceptions, most lodgepole stands in western Montana are composed of trees containing both serotinous and nonserotinous or open cones. The ratio of serotinous to nonserotinous cones seems to be related to the fire frequency for the site: the higher the fire frequency the greater the proportion of serotinous cones and vice versa (Perry and Lotan 1979).

A temperature of 113 °F (45 °C) is usually required to melt the resin that binds the scales of a serotinous cone. Heat from a fire is about the only way such temperatures will occur in the crown of a standing lodgepole pine. Large quantities of highly viable seed are therefore available to regenerate a site following a stand-destroying fire.

Aside from serotinous cones, other silvical characteristics (Fowells 1965) that contribute to lodgepole pine's success in dominating a recently burned site are:

1. Early seed production. Cones bearing viable seed are produced by trees as young as 5 years in open stands and by trees 15 to 20 years old in more heavily stocked stands. This feature not only allows relatively young stands to regenerate a site following fire, but also the seed from open cones on recently regenerated lodgepole can fill in voids left by the original postfire seeding from serotinous cones.

2. Prolific seed production. Good cone crops occur at 1- to 3-year intervals with light crops intervening.

3. High seed viability. Viable seed has been found in 80-year-old serotinous cones.

4. High survival and rapid growth. High seedling survival and rapid early growth are characteristic of lodgepole, especially on mineral soil seedbeds exposed to full sunlight.

Lodgepole pine's success in revegetating a site following fire often results in dense, overstocked stands. Such stands are susceptible to stagnation, snow breakage, windthrow, dwarf mistletoe (*Arceuthobium americanum*) infestation, and mountain pine beetle (*Dendroctonus ponderosae*) attack. The combined effect of these factors is extreme buildup of dead woody fuel on the forest floor. Thus, the stage is set for another stand-destroying wildfire.

Whitebark Pine (*Pinus albicaulis*)

Whitebark pine is a semitolerant or midtolerant species (Arno and Hoff in press) that has been observed as a pioneer inhabiting recently burned sites. It occurs as the potential climax species on alpine timberline and exceptionally dry sites but is a seral species in upper subalpine forests (Arno 1986). Whitebark pine is moderately fire resistant. It has a relatively thin bark and is susceptible to fire injury from hot surface fires that heat the tree's cambium. The characteristically dry, exposed site and open stand structure tend to reduce whitebark pine's vulnerability to fire. The fact that whitebark pine often reaches ages of 500 years or more reflects the reduced fire threat.

Near its lower elevational limit, whitebark pine may occur in small groups with lodgepole pine, subalpine fir, and Engelmann spruce. However, the general impression of whitebark pine communities is that of open stands where the undergrowth is predominantly continuous low shrubs, forbs, and grasses. Occasionally larger shrubs and stunted trees are present.

Fires that burn in the undergrowth are usually of low-to-moderate severity. But the low, ground-hugging crowns of associated conifers can provide a fuel ladder, and downfall in the vicinity of mature trees locally increases crown fire potential. Hence, severe fires are possible.

Severe wildfires starting in lower elevations can spread throughout the upper elevation forests to timberline. Although the open nature of a whitebark pine forest acts as a firebreak, many trees can be killed under these conditions. The most common fires are lightning fires that do not spread far. However, during extended dry periods of high fire danger, these usually benign fires may spread downhill into dense lower elevation forests.

Whitebark pine has a large, wingless seed that does not disperse by wind. Regeneration on burned sites is usually the result of seed germination from bird and rodent seed caches, especially those of Clark's nutcracker (*Nucifraga columbiana*) (Hutchins and Lanner 1982).

Subalpine Fir (*Abies lasiocarpa*)

Subalpine fir is rated as the least fire-resistant Northern Rocky Mountain conifer because of its thin bark, resin blisters, low and dense branching habit, and moderate-to-high stand density in mature forests. As a result, fire most often acts as a stand-replacement agent when it burns through a subalpine fir forest. Even relatively cool

ground fires can cook the cambium or spread into the ground-hugging branches and from there up into the crown.

Subalpine fir may begin producing cones when only 20 years old, but maximum seed production is by dominant trees 150 to 200 years old. Subalpine fir has the ability to germinate and survive on a fairly wide range of seedbeds.

Subalpine fir can occur in a fire-initiated stand with Douglas-fir, lodgepole pine, and other seral species because it germinates successfully on a fire-prepared seedbed. But subalpine fir usually remains a slower growing, minor component dominated by less tolerant species.

Subalpine fir can better exist under low light conditions than most associated species. But Engelmann spruce will often grow faster than subalpine fir where light intensity exceeds 50 percent of full sunlight. Subalpine fir is shade tolerant and is the indicated climax species on many sites containing lodgepole pine. Where a seed source exists, the fir will invade and grow in the understory of lodgepole stands. Given a long enough fire-free period, subalpine fir will overtop lodgepole pine on sites where it is the indicated climax.

Mountain Hemlock (*Tsuga mertensiana*)

Mountain hemlock is vulnerable to fire damage. It is only slightly more fire resistant than subalpine fir. Its thin bark affords some protection, but low-hanging branches, highly flammable needles, and a tendency to grow in dense groups make it susceptible to fire injury. Trees that survive fires often suffer subsequent mortality from fungus-infected fire wounds.

Mountain hemlock grows in pure stands or in mixtures with a variety of species. In Montana, subalpine fir, Engelmann spruce, and whitebark pine are common associates. Mountain hemlock sites are typically moist with average annual precipitation over 50 inches (127 cm), making fire occurrence low. When these forests do dry, however, fires often burn severely.

Mountain hemlock is a tolerant tree, surpassing subalpine fir in this respect. It is considered a coclimax species with subalpine fir where they occur together. Mountain hemlock seedlings and saplings survive prolonged suppression and respond well to release.

The ability of mountain hemlock to act as a pioneer species apparently varies with locality. In northern California and southern Oregon, nearly pure, even-aged stands on old burn sites have been reported. In central Oregon, British Columbia, and Alaska, it has invaded small openings, meadows, glacial moraines, and heather communities. It is an invader of burned sites in the high-elevation forests of the Northern Rocky Mountains.

Western White Pine (*Pinus monticola*)

Western white pine is moderately resistant to fire. Its resistance is favored by medium thick bark, moderately flammable foliage, self-pruning of lower limbs, and especially, its tall stature. But, older trees retain abundant resin in their bark and often have lichen-covered branches. These factors, plus the often dense stand structure, reduce western white pine's fire resistance.

Young trees are especially vulnerable because of their compact stand structure and the lack of thickened bark. Western white pine is a fire species that depends on severe fires to recycle stands and create an early successional habitat. Its common occurrence in nearly pure, even-aged stands is further evidence of colonization after fire. Soil temperature and adequate moisture appear to control germination, but light seems to have little importance because seeds can germinate in shade. Mineral surfaces provide a better seedbed than duff surfaces, but white pine seed is able to lie over in duff for 2 or 3 years then germinate upon the removal of the litter layer.

The early growth of western white pine seedlings is not rapid, but it is the fastest growing sapling and pole-sized tree in the Northern Rockies. The first 30 to 40 years are critical to the development of the stand because during this time dominance and stand composition are established. Mortality and pruning subsequently determine the fire resistance of the stand and of individual trees.

Western white pine is moderately shade tolerant and will continue to reproduce under a partial canopy of associated seral species (Douglas-fir, western larch, lodgepole pine, and perhaps grand fir). This ability and its longevity (400 to 500 years) permit it to remain as a stand component for several centuries following major disturbance.

Grand Fir (*Abies grandis*)

An individual, mature grand fir can resist low to moderately severe fires primarily because of its moderately thick bark. However, its low and dense branching habit, highly flammable foliage, heavy lichen growth, relatively shallow root system, and dense stand habit make it susceptible to fire injury and death.

Fire resistance is strongly influenced by site. Grand fir succumbs to ground fire when the duff burns deeply enough to injure the root system. On relatively dry mountain slopes where grand fir grows, the deeper root system, lighter fuel loadings, and more open stand structure make it less vulnerable. However, decay frequently enters through fire wounds.

Grand fir tolerates partial shading and is a successful invader of small openings and shrubfields. It can continue to establish in developing stands until the canopy closes.

Grand fir has rather low reproductive success. It has the lowest percentage germination of any of the associates of white pine. Damping off fungus and other biotic agents take a heavy toll of seedlings during wet seasons, and insolation and drought cause mortality during the dry summer months. Not until their third year are the seedlings well established. Young trees on dry sites or upland slopes develop tap roots, making them more resistant to drought and fire than shallow-rooted trees on more moist sites.

In partial shade, grand fir can form a considerable part of the dominant reproduction, but in full sun it is subordinate to faster growing intolerant species. Heavy competition restricts it to a role as an understory component. Suppressed trees will show some response to release, but such individuals do not attain optimal growth or stature and often develop bole rot before attaining commercial size. Grand fir does best when it retains a dominant position from the time of its initial establishment.

Western Hemlock (*Tsuga heterophylla*)

Western hemlock is easily killed by fire because of its thin bark, shallow roots, highly flammable foliage, and low-branching habit. It tends to form dense stands and its branches are often lichen-covered, which serve to increase its susceptibility to fire damage. Postburn mortality of individuals is common due to fungal infection of fire wounds.

The range of western hemlock in Montana is restricted to the northwest portion, where relatively warm, mesic conditions prevail. Except during especially long dry periods in summer, fire seldom burns these sites.

Hemlock becomes a prolific seeder at an early age. It can be an aggressive pioneer because of its quick growth in full overhead light and its ability to survive under a wide variety of seedbed conditions. The light, winged seeds can be carried a considerable distance by wind.

Hemlock is a highly tolerant climax species. It survives long periods of suppression and will respond well to release. It is often found as a codominant with western redcedar on climax or near-climax stands.

Western Redcedar (*Thuja plicata*)

Western redcedar has only low to moderate fire resistance. Its thin bark, shallow root system, and low, dense branching habit make it susceptible to fire damage. Despite this apparent low resistance, the species often survives because of its large size and tenacity if any portion of the bole isn't killed.

Western redcedar is found in the mesic to hydric environments of western Montana—a region with a modified maritime climate. These moist sites provide redcedar's best protection from fire. Riparian stringers of western redcedar may act as firebreaks. The generally moist duff found beneath redcedar does not readily burn.

Redcedar is not an aggressive pioneer species because the succulent seedling is susceptible to high soil temperatures and is slow in root development. Seedling survival on burned or unburned mineral soil is best under partial shade. Small seed size and rapid drying of organic material account for the poor germination on duff. In its favor, redcedar is a prodigious seed producer, a characteristic that enables it to enter pioneer communities at an early stage.

Western redcedar will reproduce vegetatively in old-growth stands with a high soil moisture. Adventitious roots may develop from low hanging branches, live fallen trunks, or even live branches that fall on a wet soil surface.

Western redcedar is highly shade tolerant. It can germinate, grow, and even reach maturity under low-light conditions. However, its growth is retarded by dense shade, and it responds well when competition is removed.

Western redcedar is often the indicated climax species where it occurs. It can also serve as a late-seral or coclimax tree on western hemlock sites.

Subalpine Larch (*Larix lyallii*)

Subalpine larch is a thin-barked species easily damaged by fire. However, it is moderately fire-resistant primarily

because of its stand habit. It grows only on the highest elevations inhabiting extremely rocky and generally moist and cold sites. Alpine larch can grow in pure groves, in small groups, or as isolated individuals. In the lower portion of its elevational distribution, it occurs with subalpine fir, Engelmann spruce, and whitebark pine.

In the timberline zone, fire is a cause of tree mortality but is less frequent and widespread than in contiguous forests below. Severe fires may enter the subalpine larch stands from lower forests. However, they do not always adversely affect subalpine larch stands. For example, northern Idaho's severe Sundance Fire of 1967 swept the ridges of Roman Nose Mountain burning most of the whitebark pine and killing much of the spruce and fir in the cirques, but causing only minor damage to isolated stands of subalpine larch (Arno 1970). Sparse vegetation and rocky slopes curtail the intensity of fire in these areas.

When subalpine larch grows in association with a vigorous stand of subalpine fir, Engelmann spruce, and whitebark pine, it is an intolerant seral species that dies out when overtopped by other conifers. Arno (1970) stated that fire allowed subalpine larch to remain a major forest component with these species in some areas.

UNDERGROWTH RESPONSE TO FIRE

Many of the common shrubs and herbaceous plants that grow on the forest floor of Montana forests can renew themselves from surviving plant parts following fire. Other plants are quite susceptible to fire kill and often must re-establish or colonize from off-site seed sources in unburned areas within or immediately adjacent to the burned area.

Current understanding of the process of plant succession following fire in western Montana forests and its management implications are succinctly summarized by Stickney (1982):

...the severity of the disturbance treatment directly affects the representation of the survivor component in the postfire vegetation. Since survivors derive from plants already established at the time of disturbance, it is possible, by pretreatment inventory, to determine the potential composition for the survivor component. For this reason it also follows that forest stands with little undergrowth vegetation could be expected to have a sparse or limited survivor component following disturbance. In addition, if the colonizer component is composed mostly of shade-tolerant climax-like species the rate of survivor recovery can be expected to be slow. Nearly all of our native forest shrub species are capable of surviving burning, and they can therefore be expected to function as survivors. A majority of the predisturbance forest herb species also demonstrated the ability to survive fire, particularly those species with underground stems (rhizome) or rootcrowns (caudex). As a generalization, the more severe the fire treatment to vegetation, the less the survivor component. In the drier, more open forest types this usually results in a reduction of amount, but not major changes in composition. However, in the moister forest types, where the undergrowth

is made up of more mesic shade-tolerant species, marked changes in postfire composition can occur as increasing severity reduces survivor representation.

The severity of disturbance treatment (particularly fire) influences the potential for colonizer presence in two ways: (1) the degree of severity creates the character of the ground surface on which colonizer seedlings germinate, and (2) it activates onsite stored seed. Generalizing, the more severe the disturbance treatment the more favorable the site becomes for colonizers. As the extent of exposed mineral soil increases, the ground surface becomes more favorable as a site for germination and establishment of colonizer plants. Increases in treatment severity also favor germination of ground-stored seeds by increasing their exposure to light or heat.

Predicting the occurrence of colonizers in post-disturbance vegetation is much less certain than

predicting for survivors, but knowledge of the previous succession history can provide the potential composition of residual colonizers. Locally this information is often available from an adjacent or nearby clearcut. Least predictable is the offsite colonizer component, for its occurrence is dependent on the timing of the disturbance to the availability and dispersal of offsite airborne seed. Even in this case reference to local clearcuts can provide some idea of the composition for the most common offsite colonizer species likely to occur

Table 3 is a brief summary of plant response to fire for some species that occur in western Montana forests. The fire response information is generalized. Remember, plant response to fire depends on many factors including soil and duff moisture, phenological stage of the plant, and the severity of the fire, especially in terms of the amount of heat that travels downward through the duff and upper layer of soil.

Table 3—Summary of postfire survival strategy and fire response for some shrubs and herbaceous plants occurring in forests west of the Continental Divide in Montana (sources: Arno and Simmerman 1982; Bradley 1984; Crane and others 1983; Daubenmire and Daubenmire 1968; Hironaka and others 1983; Kramer 1984; Lotan and others 1981; Lyon and Stickney 1976; McLean 1969; Miller 1977; Morgan and Neuenschwander 1985; Mueggler 1965; Nimir and Payne 1978; Noste 1985; Rowe 1983; Stickney 1981; Tiedemann and Klock 1976; Volland and Dell 1981; Wright 1980, 1978, 1972; Wright and Bailey 1982, 1980; Wright and others 1979)

Species	Fire Group(s)	Postfire survival strategy	Comments on fire response
SHRUBS:			
<i>Alnus sinuata</i> Sitka alder	6,8,9,10,11	Sprouts from surviving root crown.	Usually increases on site following fire. Early seed production (after 5 years) aids in this increase.
<i>Amelanchier alnifolia</i> Western serviceberry	ubiquitous ¹	Sprouts from surviving root crown, frequently producing multiple stems.	Pioneer species; usually survives even severe fires especially if soil is moist at time of fire. Coverage usually increases following fire.
<i>Arctostaphylos uva-ursi</i> Kinnikinnick	ubiquitous	May sprout from a root crown; regeneration from stolons more common. May have somewhat fire-resistant seeds.	Susceptible to fire-kill. Will survive some low severity fires when duff is moist and therefore not consumed by fire. May invade burned area from unburned patches.
<i>Artemisia tridentata</i> Big sagebrush	1,2,4,5	Wind-dispersed seed. Subspecies <i>vaseyana</i> stores seed in the soil that germinates as a result of fire-induced heating.	Susceptible to fire-kill. Recovery is hastened when a good seed crop exists before burning.
<i>Berberis repens</i> Creeping Oregon grape	ubiquitous	Sprouts from surviving rhizomes that grow 0.5 to 2 inches (1.5 to 5 cm) below soil surface.	Moderately resistant to fire-kill. Usually survives all but severe fires that remove duff and cause extended heating of upper soil.
<i>Ceanothus velutinus</i> Snowbrush ceanothus	2,4,5,6,7,8,9,11	Soil-stored seed germinates following heat treatment. It can also sprout from root crowns following a cool fire.	Usually increases following fire, often dramatically.
<i>Cornus canadensis</i> Bunchberry dogwood	5,6,7,9,11	Sprouts from surviving rhizomes that grow 2 to 5 inches (5 to 13 cm) below soil surface.	Moderately resistant to fire-kill. Will survive all but severe fires that remove duff and cause extended heating of upper soil.
<i>Cornus stolonifera</i> Redosier dogwood	6,9,11	Sprouts from surviving rhizomes or stolons (runners).	Susceptible to fire-kill. Will survive all but severe fires that remove duff and cause extended heating of upper soil.
<i>Holodiscus discolor</i> Oceanspray	4,6,9,11	Regenerates from soil-stored seed or sprouts from surviving root crown.	Moderately resistant to fire-kill. Is often enhanced by fire.
<i>Juniperus communis</i> Common juniper	1,4,5,6,7,8,10	Bird-dispersed seed.	Susceptible to fire-kill. Seed requires long germination period.

(con.)

Table 3 (Con.)

Species	Fire Group(s)	Postfire survival strategy	Comments on fire response
<i>Juniperus horizontalis</i> Creeping juniper	1,2,5	Similar to <i>J. communis</i> .	See <i>J. communis</i> .
<i>Linnaea borealis</i> American twinflower	6,7,8,9,11	Sprouts from surviving root crown located just below soil surface. Fibrous roots and runners at soil surface.	Susceptible to fire-kill. May survive some cool fires where duff is moist and not consumed. Can invade burned area from unburned patches.
<i>Lonicera utahensis</i> Utah honeysuckle	4,5,6,7,8,9, 10,11	Sprouts from surviving root crown.	Often a reduction in cover and frequency following fire.
<i>Menziesia ferruginea</i> Rusty menziesia	6,9,10,11	Sprouts from surviving root crown.	Susceptible to fire-kill. Moderate to severe fires reduce survival and slow redevelopment.
<i>Oplopanax horridum</i> Devil's club	9,11	May sprout from root crown.	Susceptible to fire-kill.
<i>Pachystima myrsinites</i> Mountain lover	6,8,9,10,11	Sprouts from surviving root crown and from buds along taproot.	Moderately resistant to fire-kill. Usually survives low to moderate severity fires that do not consume the duff and heat soil excessively. Usually increases.
<i>Philadelphus lewisii</i> Lewis mockorange	0,1,2,4,5,11	Sprouts from root crown.	Fire resistant; a vigorous resprouter.
<i>Physocarpus malvaceus</i> Mountain ninebark	0,1,2,4,5,6,8, 9,11	Sprouts from surviving root crown or horizontal rhizomes.	Fire resistant. Resprouts well although spreading may be somewhat delayed.
<i>Potentilla fruticosa</i> Shrubby cinquefoil	0,1,2,4,5,8,9, 10	Sprouts from surviving root crown	Susceptible to fire-kill, but may survive low to moderate fires.
<i>Prunus virginiana</i> Chokecherry	0,1,2,4,5,6,7, 9	Sprouts from surviving root crown; occasionally from rhizomes.	Usually increases coverage following fire.
<i>Purshia tridentata</i> Antelope bitterbrush	1,2,4,5,6,7	A weak sprouter. Animal-dispersed seed and seed caches present on area prior to fire.	Susceptible to fire-kill, especially in summer and fall. Decumbent growth form sprouts vigorously, columnar form does not. Spring burns enhance sprouting, fall burns are best for regeneration by seed.
<i>Ribes lacustre</i> Prickly currant	1,4,7,8,9	Sprouts from surviving root crown that is located beneath soil surface.	Resistant to fire-kill. Usually increases even after severe fire. Seedlings may establish after low or moderate fires.
<i>Rubus parviflorus</i> Thimbleberry	6,7,8,9,11	Sprouts from surviving rhizomes; seedlings from soil-stored and possible bird-dispersed seed.	Spreads vigorously from rhizomes; rapid recovery after fire.
<i>Salix scouleriana</i> Scouler willow	6,7,8,9,10,11	Sprouts from root crown/caudex. Has numerous wind-borne seeds.	Resprouts vigorously after fire and seeds germinate readily on moist burned sites.
<i>Shepherdia canadensis</i> Russet buffaloberry	1,4,5,7,8,9, 10,11	Sprouts from surviving root crown and from buds along taproot.	Moderately resistant to fire-kill. Will usually survive cool to moderately severe fires that fail to consume duff and heat soil extensively.
<i>Sorbus scopulina</i> Greene mountainash	6,7,8,9,10,11	Sprouts from deep-seated rhizomes.	Resprouts vigorously after fire.
<i>Spiraea betulifolia</i> White spirea	3,4,5,6,7,8 ubiquitous	Sprouts from surviving root crown and from rhizomes that grow 2 to 5 inches (5 to 13 cm) below surface.	Resistant to fire-kill. Will usually survive even a severe fire. Generally increases coverage following fire.
<i>Symphoricarpos albus</i> Common snowberry	2,3,4,6,7,8,9 ubiquitous	Sprouts vigorously from surviving rhizomes that are located between 2 and 5 inches (5 to 13 cm) below soil surface.	Resistant to fire-kill. Will usually survive even severe fires. Greatly enhanced by cool to moderately severe fires.
<i>Taxus brevifolia</i> Pacific yew	9,11	Bird-dispersed seed.	Easily killed by fire because of thin bark.
<i>Vaccinium globulare</i> Blue huckleberry	0,6,7,8,9,10, 11	Shallow and deep rhizomes.	Moderately resistant to fire-kill. Will usually survive cool to moderately severe fires.
<i>Vaccinium scoparium</i> Grouse whortleberry	6,7,8,9,10,11	Sprouts from surviving rhizomes that grow in duff layer or at surface of soil.	Moderately resistant to fire-kill. Will usually survive cool to moderately severe fires that fail to consume the lower layer of duff.

(con.)

Table 3 (Con.)

Species	Fire Group(s)	Postfire survival strategy	Comments on fire response
FORBS:			
<i>Adenocaulon bicolor</i> American trailplant	6,7,9,11	Sprouts from rhizomes near mineral soil surface.	Moderately susceptible to fire-kill. May survive moderately severe fires that fail to consume lower duff.
<i>Apocynum androsaemifolium</i> Spreading dogbane	2,4,5,6,7,	Sprouts from surviving rhizomes.	Generally maintains prefire frequency following fire.
<i>Aralia nudicaulis</i> Wild sarsaparilla	6,9,11	Sprouts from surviving rhizomes.	Generally resistant to fire-kill.
<i>Arnica cordifolia</i> Heartleaf arnica	ubiquitous	Sprouts from surviving rhizomes that creep laterally from 0.4 to 0.8 inches (1 to 2 cm) below soil surface. Wind-dispersed seed.	Susceptible to fire-kill. Shoots produce small crowns within the duff that are easily killed by all but cool fires that occur when duff is moist. May rapidly invade burned area via wind-borne seed.
<i>Arnica latifolia</i> Broadleaf or mountain arnica	4,5,6,7,8,9,10,11	Sprouts from surviving rhizomes that creep laterally in the soil.	Susceptible to fire-kill. Will usually survive cool to moderately severe fires. May exhibit rapid initial regrowth accompanied by heavy flowering and seeding establishment.
<i>Aster conspicuus</i> Conspicuous aster	1,2,4,6,7,8,9,10,11	Sprouts from surviving rhizomes that mostly grow from 0.5 to 2 inches (1.5 to 5 cm) below soil surface.	Moderately resistant to fire-kill. Will usually survive cool to moderately severe fires that do not result in excessive soil heating. May rapidly increase following fire.
<i>Astragalus miser</i> Timber milkvetch	0,1,2,4,5,7,8,9,10,11	Sprouts from buds along surviving taproot that may be 2 to 8 inches (5 to 20 cm) below root crown.	Resistant to fire-kill. Can regenerate from taproot even when entire plant crown is destroyed. Can send up shoots and set seed the first year. May increase dramatically following fire. Note: Milkvetch is poisonous to sheep and cattle.
<i>Balsamorhiza sagittata</i> Arrowleaf balsamroot	0,1,2,4,5,6,8,10	Regrowth from surviving thick caudex.	Resistant to fire-kill. Will survive even the most severe fire.
<i>Chimaphila umbellata</i> Prince's pine	6,7,8,9,10,11	Rhizomes in duff near mineral soil surface.	May survive moderate fires that do not thoroughly heat duff.
<i>Clintonia uniflora</i> Queencup beadlily	6,8,9,11	Sprouts from surviving rhizomes.	Usually decreases following fire. Postfire environment evidently not conducive to rapid recovery.
<i>Fragaria virginiana</i> Virginia strawberry	ubiquitous	Sprouts from surviving stolons (runners) at or just below soil surface.	Susceptible to fire-kill. Will often survive cool fires that do not consume duff because of high duff moisture content.
<i>Galium triflorum</i> Sweetscented bedstraw	6,7,8,9,11	Sprouts from surviving rhizomes; barbed, animal-borne seeds.	Susceptible to fire-kill. Usually a sharp decrease following severe fire. Can increase following spring and fall fires.
<i>Osmorhiza chilensis</i> Mountain sweetroot	ubiquitous	Short shallow roots; barbed, animal-dispersed seeds.	Moderately fire resistant; temporary increase after fire.
<i>Pyrola secunda</i> Sidebells shineleaf	1,5,6,8,9,10,11	Sprouts from surviving rhizomes that grow mostly in the duff or at soil surface.	Susceptible to fire-kill. Coverage frequently reduced following fire. May survive cool fires when duff moisture is high.
<i>Smilacina racemosa</i> False Solomon's seal	ubiquitous	Sprouts from surviving stout creeping rhizomes.	Moderately resistant to fire-kill. May be killed by severe fires that remove duff and heat soil excessively. Usually maintains prefire frequency.
<i>Smilacina stellata</i> Starry false Solomon's seal	ubiquitous	Sprouts from surviving creeping rhizomes.	Moderately resistant to fire-kill. May be killed by fires that remove duff and heat upper soil. Frequency often reduced following fire.
<i>Thalictrum occidentale</i> Western meadowrue	0,1,4,5,6,7,8,9,11	Sprouts from surviving rhizomes.	Susceptible to fire-kill. Frequency usually reduced following fire. May survive cool fires that do not consume duff.

(con.)

Table 3 (Con.)

Species	Fire Group(s)	Postfire survival strategy	Comments on fire response
<i>Xerophyllum tenax</i> Common beargrass	0,6,7,8,9,10, 11	Sprouts from a surviving stout shallow rhizome.	Susceptible to fire-kill. Will survive cool fires that do not consume lower duff. Resprouts will flower vigorously after a fire until new overstory canopy develops.
<i>Zygadenus elegans</i> Mountain deathcamas	0,1,2,4,5,6,7, 8,9,10	Sprouts from surviving tunicated bulb.	Resistant to fire-kill.
GRASSES:			
<i>Agropyron spicatum</i> Bluebunch wheatgrass	1,2,4,5	Seed germination and some sprouts from surviving rhizomes.	Usually not seriously damaged by fire. Response depends on severity of fire and physiological state of plant. Damage will be greatest following dry year.
<i>Calamagrostis rubescens</i> Pinegrass	0,2,4,5,6,7,8, 9,10,11	Sprouts from surviving rhizomes that grow within the top 2 inches (5 cm) of soil.	Moderately resistant to fire-kill. Will usually survive cool to moderately severe fires that do not completely consume duff. Burned areas are often successfully invaded by pinegrass.
<i>Carex geyeri</i> Elk sedge	ubiquitous	Sprouts from surviving rhizomes.	Invades burned areas and forms dense stands. Often increases following fire.
<i>Carex rossii</i> Ross sedge	ubiquitous	Seed stored in duff or soil that germinates when heat treated. Sprouts from surviving rhizomes.	Increased coverage usually results following most fires severe enough to heat but not completely consume duff. Often increases.
<i>Festuca idahoensis</i> Idaho fescue	1,2,4,5,6,7,8, 9	Seed germination and survival of residual plant.	Susceptible to fire-kill. Response will vary with severity of fire and physiological state of plant. Can be seriously harmed by hot summer and fall fires. Only slightly damaged during spring or fall when soil moisture is high.
<i>Festuca scabrella</i> Rough fescue	1,2,4,5,6,7,8, 9,10	Seed germination and residual plant survival.	Usually harmed by spring burning.
<i>Koeleria cristata</i> Junegrass	1,2,4,5,6,7,8	Seed germination and residual plant survival.	Susceptible to fire-kill. Response will vary according to fire severity and physiological state of plant.
<i>Luzula hitchcockii</i> Woodrush	7,9,10	Sprouts from surviving rhizomes.	Often a slight increase following fire.

¹"Ubiquitous" denotes species whose distribution includes 10 or more Fire Groups and many or most habitat types within those Fire Groups.

WILDLIFE RESPONSE TO FIRE

The effects of fire on wildlife are primarily secondary effects. Fire creates, destroys, enhances, or degrades favorable wildlife habitat (food supply, cover, shelter, physical environment), thereby causing changes in the subsequent occurrence and abundance of animal species on a burned area (fig. 2). Table 4 lists the probable effects of fire on some mammals, reptiles, and amphibians in western Montana forests. The indicated fire effects are either inferred from habitat requirements or from studies conducted on specific wildfire or prescribed fire areas. Keep in mind that a major problem in attempting any generalization about the effects of fire on wildlife is the variation in fires: intensity, duration, frequency, location, shape, extent, season, fuels, sites, soils, and prescribed fires as compared to wildfires (Lyon and others 1978).

The response of bird species to fire has been hypothesized by Kramp and others (1983) using a classification suggested by Walter (1977).

Four fire response categories are recognized in this classification: fire-intolerant, fire-impervious, fire-adapted, and fire-dependent. These classes are described as follows (Kramp and others 1983):

Fire-intolerant species decrease in abundance after fire and are present only in areas characterized by very low fire frequency and severity. Characteristic western Montana species include the hermit thrush, red-breasted nuthatch, and brown creeper, which are closely associated with closed canopy forests. These birds prefer a dense

nesting and foraging cover but do not use fire-opened habitat.

Fire-impervious bird species are unaffected by fire; they neither increase nor decrease because of fire. Bird species whose niche incorporates successional and climax community types may be expected to show the highest flexibility in response to fire.

Fire-adapted species are associated with habitat that is characterized by recurring fires of various severity. These species, however, are not dependent on fire-influenced habitat. Fire-adapted species may also occupy areas with the same frequency-severity ratio as fire intolerant species. Fire-adapted birds include those that use both dense canopy areas and openings; a predator such as the sharp-shinned hawk is an example. Such birds benefit by increased hunting success in recent burns, but generally depend on unburned habitat for nesting sites.

Fire-dependent species are associated with fire-dependent and fire-adapted plant communities. When fire frequency decreases, these plant communities shift to fire-neutral or fire-intolerant types, and fire-dependent species are unable to persist. The blue grouse might be a western Montana example. The bird depends on medium to large fire-created forest openings with shrub-grass-forb vegetation for breeding adjacent to dense foliage conifers for roosting and hooting.

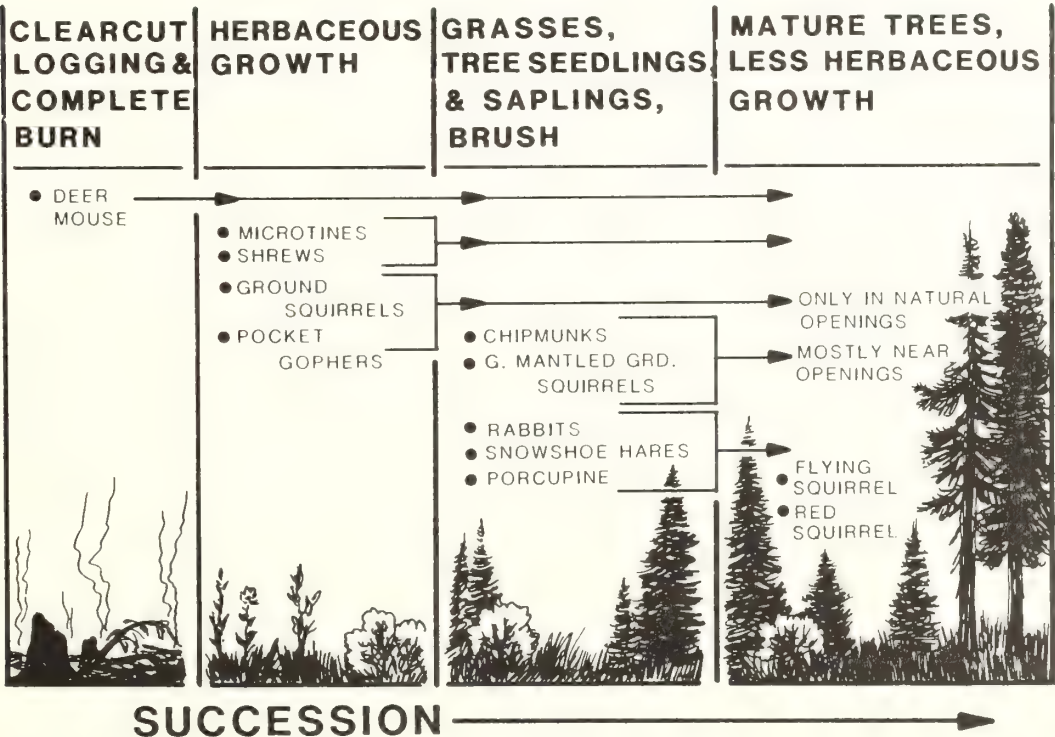


Figure 2—Small mammals found in the successional stages after clearcut logging and burning (from Ream and Gruell 1980).

Table 4—Probable effects of fire on some western Montana mammals, reptiles, and amphibians (major sources: Allen 1983; Bendell 1974; Bernard and Brown 1977; Black and Tabor 1977; Halvorsen 1981, 1982; Hobbs and Spowart 1984; Kelsall and others 1977; Lyon and others 1978; Maser and others 1981; Ream 1981; Ream and Gruell 1980; Thomas 1979; USDA Forest Service 1978; Verner and Bass 1980; Wright and Bailey 1982). Classification, scientific names, and common names according to USDA Forest Service (1978).

Species	Fire Groups	Habitat considerations	Fire effects
INSECTIVORA (insect eaters)			
Masked shrew <i>Sorex cinereus</i>	4,5,6,7,11	Prefers moist situations in forest or open. Requires a mat of ground vegetation for cover; stumps, logs, and slash piles for nest sites.	May be temporarily eliminated from severe burns where duff and ground cover are absent. Some direct mortality of nestlings possible.
Vagrant shrew <i>S. vagrans</i>	2,4,5,6,7,8, 9,10,11	Prefers streamsid es, marshes, and bogs, but also occurs in moist soil; mat of ground vegetation or debris for cover. Stumps, rotten logs for feeding and nesting.	May be temporarily eliminated from severe burns where duff, ground cover, and debris are absent. Some direct mortality of nestlings possible.
CHIROPTERA (bats)			
Little brown myotis <i>Myotis lucifugus</i>	2,7,8,9,10	Common in forest and at the forest edge. Requires snags and tree holes for roosting and for maternity colony sites.	Severe fires may destroy roosting and breeding sites. Relatively impervious to cool and moderate fires.
Long-eared myotis <i>M. evotis</i>	2,4,5,6,7,8, 9,10	Occurs in coniferous woodland as well as in spruce-fir zone. Uses snags and tree holes for roosting and for breeding colonies.	Severe fires may destroy roosting and breeding sites; otherwise relatively impervious to fire.
Small-footed myotis <i>M. subulatus</i>	2,7,8,9,10	Most common in ponderosa pine zone. May use hollow trees and snags for roosting and breeding.	Severe fires may destroy roosting and breeding sites but with little impact on populations.
Long-legged myotis <i>M. volans</i>	2,4,5	Prefers open coniferous forests. May use tree cavities for roosting and breeding.	Severe fires may destroy roosting and breeding sites but with little impact on populations.
Silver-haired bat <i>Lasionycteris noctivagrans</i>	2,4,5	Feeds in openings and adjacent to mature forest. Roosts in tree foliage; uses hollow trees and snags for breeding.	Severe fires may destroy some roosting and breeding sites. Relatively impervious to fire.
Big brown bat <i>Eptesicus fuscus</i>	2,4,5	Common over grassy meadows surrounded by ponderosa pine. Roosts and breeds in hollow trees and snags.	Severe fires may reduce breeding and roosting sites. Relatively impervious to fire.
Western big-eared bat <i>Plecotus townsendii</i>	2,7,8,9,10	May be found in forests up through spruce-fir zone. Not a tree user.	Relatively impervious to fire.
Hoary bat <i>Lasiurus cinereus</i>	2,4,5	Prefers wooded areas and trees with dense foliage for roosting and breeding.	Severe fires can destroy roosting and breeding sites. Cool fires have little effect on populations.
LAGOMORPHA (pikas, hares, and rabbits)			
Pika <i>Ochotona princeps</i>	2,4,5,6,7,8, 9,10,11	Prefers high-altitude talus slopes adjacent to forest openings containing grasses and forbs.	Relatively impervious to fire. Severe fires may create favorable forest openings with abundant grass-forb food supply.
Mountain cottontail <i>Sylvilagus nuttalli</i>	2	Prefers dense shrubby undergrowth and pole-sized trees for cover. Uses downed logs for cover and nest sites.	Temporarily eliminated from severe burns but reoccupy as shrub cover increases. Will continue to use less than severe burns.
Snowshoe hare <i>Lepus americanus</i>	4,5,6,7,8,9, 10,11	Prefers dense shrubs in forest openings or under pole-sized trees for food and cover. Uses downed logs for cover and nest sites.	Temporarily eliminated from severe burns. Populations may increase dramatically as shrubs resprout and dominate the area. Will continue to use less than severe burns.
RODENTIA (gnawing mammals)			
Least chipmunk <i>Eutamias minimus</i>	7,8,9,10	Present in high mountain coniferous forests. Requires open areas with stumps, downed logs, and shrubs or other high vegetation for cover.	Temporarily decreases following severe fire that reduces cover. Return first season after fire and usually abundant by third postfire year.

(con.)

Table 4 (Con.)

Species	Fire Groups	Habitat considerations	Fire effects
Redtail chipmunk <i>E. ruficaudus</i>	2,4,5,6,7,8, 9,10,11	Most common in forest openings or edges with abundant shrub undergrowth.	May be temporarily reduced or eliminated on severe burns lacking cover. Use of moderate burns may continue at reduced level, especially if cover and fresh seed is abundant. Populations may exceed pre-burn levels by second or third postfire year.
Yellowpine chipmunk <i>E. amoenus</i>	2,4,5,6,7,8, 9,10,11	Prefers shrub, seedling, and sapling stages of forest succession. Usually abundant in open ponderosa pine forests and edges. Needs shelter of downed logs, debris, or shrubs. Often burrows under downed logs and stumps.	Recent burns with stumps and shrubs are favored habitat, especially as seed and fruit producing annuals become available.
Yellow-bellied marmot <i>Marmota flaviventris</i>	2,4,5,6,7,8, 9,10,11	Prefers rocky outcrops or talus slopes; forest openings up through spruce-fir zone. Uses downed logs for cover; burrows under tree roots. Feeds on green grass and forbs.	Relatively impervious to fire. Benefits from fire-created openings dominated by grass and forbs.
Hoary marmot <i>M. caligata</i>	6,7,8,9,10	Found in alpine and subalpine habitats; on talus slopes near grassy alpine meadows.	Relatively impervious to fire. Benefits from fire-created grassy openings.
Uinta ground squirrel <i>Spermophilus armatus</i>	4,5,6,7,8,9, 10	Prefers moist habitats with lush vegetation and soft soil; subalpine meadows; forest edges.	May increase dramatically on areas where fire has killed overstory. May be favored by increased light and temperature as well as increase in herbaceous growth.
Columbian ground squirrel <i>S. columbianus</i>	2,4,5,6,7,11	Prefers subalpine meadows, forest edges, open woodlands, pine flats, and alpine tundra. Uses downed logs for cover. Burrows on rocky, partly forested gentle slopes.	May increase on areas where canopy has been opened by fire, especially if grass, forbs, and seed are abundant.
Golden-mantled squirrel <i>S. lateralis</i>	2,4,5,6,7,8, 9,10,11	Widespread from ponderosa pine forest to alpine meadows. Most abundant in open forests lacking a dense undergrowth or understory. Needs downed logs, stumps, or rocks for cover. Burrows for shelter.	Generally increases on recently burned areas due to increased abundance of forbs, providing adequate escape cover exists.
Red squirrel <i>Tamiasciurus hudsonicus</i>	2,4,5,6,7,8, 9,10,11	Found in late successional forests. Nests in tree cavities and branches. Feeds on conifer seeds, nuts, bird eggs, fungi. Uses downed logs for cover.	Essentially eliminated following stand-replacing fires. Cavities in fire-killed trees may be used for dens but only if surrounded by live trees.
Northern flying squirrel <i>Glaucomys sabrinus</i>	2,4,5,6,7,8, 9,10,11	Prefers a mature forest. Requires snags and trees with nest cavities. Also requires an abundance of downed logs. Feeds on conifer seed, serviceberries, and mushrooms.	Same as for red squirrel except may forage for fungi in recent burns.
Northern pocket gopher <i>Thomomys talpoides</i>	2,4,5,6,7,8, 9,10,11	Prefers disturbed areas of secondary vegetative growth; also pine forests, alpine parks, and meadows. Occurs mostly in deep sandy soils but also in clay and gravelly soils. Requires an herbaceous food source, especially annual forbs.	Population densities usually increase on areas burned by fires that open canopy and disturb the soil resulting in undergrowth of early successional forbs and grasses.
Beaver <i>Castor canadensis</i>	All	Requires streams or lakes bordered by stands of aspen, alder, birch, poplars, or willow for food and building materials.	Populations usually increase following fires that initiate a successional sequence that includes aspen as an intermediate stage.
Western harvest mouse <i>Reithrodontomys megalotis</i>	All	Generally restricted to grass-forb stages on all habitat types. Usually nests on ground but sometimes in woodpecker holes.	Generally favored by fires that result in establishment of seed-producing annual plants.

(con.)

Table 4 (Con.)

Species	Fire Groups	Habitat considerations	Fire effects
Deer mouse <i>Peromyscus maniculatus</i>	All	Ubiquitous. Occurs in most successional stages of most habitat types. Nests in burrows, trees, and stumps. Uses downed logs for nesting sites and cover.	Populations reduce immediately following fire but significantly increase as soon as rain settles the ash. Most abundant small mammal on severely burned areas.
White-footed mouse <i>P. leucopus</i>	2,3,4	Found in riparian woodlands, pine, and aspen; brushy areas; in grasslands below woodlands. Burrows in sandy soils but may nest in old bird or squirrel nests, or under stumps and logs.	Response to fire similar to that of deer mouse. Preferred habitat less likely to experience severe fire.
Bushytail woodrat <i>Neotoma cinerea</i>	2,4,5,6,7,8, 9,10,11	Prefers rocky situations. Dens in rock crevices; sometimes in hollow logs. Gathers conifer seed, berries, fungi, twigs, shoots, and green vegetation.	Relatively impervious to fires that occur in high-elevation rocky habitat. Usually not abundant on recent burns.
Southern red-backed mouse (boreal red-backed vole) <i>Clethrionomys gapperi</i>	2,4,5,6,7,8, 9,10,11	Prefers mesic areas within coniferous forests that contain abundance of large debris on forest floor and undergrowth of shrubs and herbs. Feeds on conifer seed, bark, fungi, and green vegetation. A coniferous overhead tree canopy is preferred.	Usually eliminated from severely burned areas within 1 year after fire. If overstory trees are present and survive, favorable habitat may return in 7 or more years after the fire.
Mountain phenacomys (heather vole) <i>Phenacomys intermedius</i>	2,4,5,6,7,8, 9,10,11	Found in both dry and moist habitats; in grassy areas and in shrub patches in conifer forests. Burrows under stumps or downed logs. Feeds on seeds, bark, green vegetation, lichens, and berries.	Probably eliminated from severe burns. Reinvades with the establishment of suitable cover.
Meadow vole <i>Microtus pennsylvanicus</i>	2,4,5,6,7,8, 9,10,11	Requires a mat of ground cover for runways, palatable herbs, conifer seed, and moisture. Uses downed logs for cover and nest sites. Usually found near streamside.	Usually eliminated from severe burns where surface organic layer is absent. The wet nature of preferred habitat tends to resist fire.
Longtail vole <i>M. longicaudus</i>	2,4,5,6,7,8, 9,10	Widespread in wet mountain meadows and forest edge, often near streams. Requires a grass-sedge-forb food source. Less restricted to runways and dense grass than other <i>Microtus</i> .	Use increases with removal of tree canopy especially on moist north slopes.
Muskrat <i>Ondatra zibethicus</i>	Wide range	Occupies cattail marshes; banks of ponds, lakes, or slow-moving streams. Requires a source of succulent grasses or sedges, or other aquatic vegetation.	Periodic fire retains marshes in a subclimax state and removes unfavorable vegetation that crowds out useful plants.
Western jumping mouse <i>Zapus princeps</i>	2,4,5,6,7,8, 9,10,11	Requires a well-developed extensive herbaceous layer along edge of rivers, streams, lakes, or other wet areas and moist soil. Uses downed logs for cover and nest sites. Eats seed, grass, and forbs.	Generally eliminated from severe burns that lack the required vegetative cover.
Porcupine <i>Erethizon dorsatum</i>	4,5,6,7,8,9, 10,11	Prefers medium and old-age conifer stands of less than 70 percent crown closure and containing shrubs and herbs. Uses hollow logs and tree cavities for dens.	Use of severely burned areas curtailed especially if overstory is killed. May continue to use light and moderate burns.
CARNIVORA (flesh-eaters)			
Coyote <i>Canis latrans</i>	All	Widespread occurrence in most habitats and most successional stages. Uses hollow logs or stumps for dens. Preys on mice.	Increased use of burned areas that support abundant small mammal populations.
Gray wolf <i>C. lupus</i>	4,5,6,7,8,9, 10	Highly adaptable but probably restricted to wilderness forests. Preys on other mammals.	Probable increased use of burned areas that support an abundant population of prey species.

(con.)

Table 4 (Con.)

Species	Fire Groups	Habitat considerations	Fire effects
Red fox <i>Vulpes fulva</i>	2,4,5,6,7,8, 9,10,11	Prefers open areas in or near forest. Uses hollow stumps and logs for dens. Food includes berries, insects, birds, rodents, squirrels, rabbits, and other small mammals.	Benefits from fires that create favorable habitat for small mammal prey species, especially those that enhance snowshoe hare populations.
Black bear <i>Ursus americanus</i>	4,5,6,7,8,9, 10	Prefers mature forests mixed with shrub-fields and meadows. Omnivorous—eats what is available. Requires windfalls, excavated holes, or uprooted or hollow trees for den sites.	Benefits from abundant regeneration of berry-producing shrubs following fire.
Grizzly bear <i>U. horribilis</i>	2,4,5,6,7,8, 9,10,11	Uses all available habitat but prefers early successional stages for feeding and mature forest for cover. Occurrence is increasingly restricted to wilderness-type lands.	Seral forest communities maintained by fire are important for preferred berry-producing plants.
Raccoon <i>Procyon lotor</i>	Widespread	Very adaptable to environmental change; in riparian situations; along marshes, streams, and lakes. Uses hollow trees and downed logs for dens. Omnivorous.	Relatively impervious to fire because of mobility and wide ecological amplitude.
Marten <i>Martes americana</i>	2,3,5,6,7,8, 9,10,11	A forest dweller; requires relatively dense climax or near-climax situation. Uses tree or snag cavities and hollow stumps for nest sites. Food includes tree squirrels, chipmunks, mice, berries, and insects.	Eliminated from severely burned stands. Benefits from vegetative mosaics resulting from periodic small fires because of increased food supply. Burns containing adequate cover may be used for feeding during summer and fall.
Fisher <i>M. pennanti</i>	2,4,5,6,7,8, 9,10,11	Prefers forest of large trees with many windfalls and downed logs. Nests in tree holes, hollow logs, and snags. Eats squirrels, porcupines, woodrats, mice, rabbits, insects, and berries.	Preferred habitat is adversely affected by severe fire. Benefits from increase in prey species on burns adjacent to favorable habitat. Adapts better to early successional stages than marten.
Ermine (shorttail weasel) <i>Mustela erminea</i>	2,4,5,6,7,8, 9,10,11	Prefers mature dense forest for breeding and resting; meadows or other forest openings for hunting. Dens often located in hollow logs and snags. Voles are an important prey; also mice, shrews, and chipmunks.	Adversely affected by severe fire that removes ground debris or kills overstory trees. Benefits from increased biomass of prey species that usually results on fire-created grass-forb successional stages.
Longtail weasel <i>M. frenata</i>	Wide range	Ubiquitous—common in most habitats. Prefers open areas and young pole stands. Den sites include logs, stumps, and snags. A major predator of voles and mice; also gophers, chipmunks, birds, insects, and vegetation.	Benefits from increased biomass of prey species that usually result on recently burned areas.
Mink <i>M. vison</i>	Wide range	May occur in any habitat containing fish-supporting marshes, lakes, and streams. Hollow logs and tree stumps along streams may be used for den sites.	Relatively impervious to most fires. May be adversely affected where fire removes streamside cover and debris.
Wolverine <i>Gulo luscus</i>	4,5,6,7,8,9, 10,11	Prefers moderate to dense forests containing large trees. Uses logs and snags as den sites. Prey includes marmots, gophers, squirrels, birds, insects; also eats fruit.	Adversely affected by fire that destroys preferred habitat but benefits from increased biomass of prey species on nearby burns.
Badger <i>Taxidea taxus</i>	Wide range	Grass-forb stages of conifer forest succession are a preferred habitat. Likes deep, friable soil for burrow excavation and rodent capturing.	Benefits from fires that result in grass-forb successional stages because of the abundant rodent populations that are often present.

(con.)

Table 4 (Con.)

Species	Fire Groups	Habitat considerations	Fire effects
Striped skunk <i>Mephitis mephitis</i>	Wide range	Prefers early successional stages of forest, but may be found in all stages and cover types. Uses hollow logs, stumps, and snags for den sites. Food includes large insects and small rodents.	Relatively impervious to fire. Benefits from increased biomass of prey species that usually occur on severe burns.
River otter <i>Lutra canadensis</i>	Wide range	Occurs along streams, marshes, and lakes. Dens in bank. Aquatic.	Essentially impervious to fire.
Mountain lion (cougar, puma) <i>Felis concolor</i>	2,4,5,6,7,8, 9,10,11	Found throughout all habitat types and successional stages. Highly mobile. Hunts deer, hares, rodents, and porcupines.	Often flourish on recently burned areas due to increased prey availability.
Lynx <i>Lynx canadensis</i>	4,5,6,7,8,9, 10	Primarily in dense coniferous forests at higher elevations. May den in hollow logs. Snowshoe hare is an important prey species.	Benefits from fire-initiated shrub stages of succession that support large populations of snowshoe hare.
Bobcat <i>L. rufus</i>	Widespread	Found in most habitats and successional stages; shrub-sapling stages are especially desirable. May establish den under large logs or in hollow logs. Preys on rodents, reptiles, and invertebrates.	Relatively impervious to fire. Benefits from any fire-induced increase in availability of prey species.
ARTIODACTYLA (even-toed hoofed mammals)			
Elk <i>Cervus canadensis</i>	4,5,6,7,8,9, 10,11	Prefers semiopen forest but with areas of dense cover for shelter. Requires food supply of grass, forbs, and shrubs, especially Scouler willow, maple, serviceberry, redstem, and bitter cherry.	Severe burns usually experience a decline in first year use; then an increase as preferred browse species become available. Moderate fires in forest may remove ground debris and other obstructions to movement.
Mule deer <i>Odocoileus hemionus</i>	Wide range	Occupies a wide range of habitats including open montane and subalpine coniferous forest; forest edges, woodlands, and shrubfields. Shrub-seedling-sapling stage of succession preferred. Needs trees and shrubs for cover on winter range. Preferred food includes tender new growth of palatable shrubs—ceanothus, cherry, mountain-mahogany, bitterbrush; many forbs and some grasses.	Fire may improve winter nutrition in grassland and mountain shrub communities by increasing the amount of green grasses. Often a decline in use during first post-burn year and then an increase in subsequent years.
Whitetail deer <i>O. virginianus</i>	Widespread	Prefers dense forest; rough, open shrublands; thickets along streams and woodlands. Diet includes shrubs, twigs, fungi, grasses, and forbs.	Fire-initiated early successional stages supporting new growth of grasses, forbs, and shrubs provide a preferred food source.
Moose <i>Alces alces</i>	All	Prefers subclimax forests with lakes and swamps. Ideal habitat includes a mosaic of numerous age classes and distribution of aspen and associated trees and shrubs within the wintering range.	Fires that result in abundant aspen and willow regeneration create a preferred habitat. Optimal successional stage occurs from 11 to 30 years following a severe fire.
Mountain goat <i>Oreomnos americanus</i>	4,5,6,7,8,9, 10,11	Frequents alpine and high subalpine zones; on steep slopes. Feeds on grasses, sedges, and shrubs.	Relatively impervious to fire; usually above fire-prone forest areas. Fire that sweeps up through subalpine and alpine forests may create favorable goat range.
Bighorn sheep (mountain sheep) <i>Ovis canadensis</i>	4,5,6,7,8,9, 10	Preferred habitat characterized by rugged rocky mountain slopes with sparse trees and adjacent to alpine meadows. Feeds on alpine shrubs and forbs in summer; shrubs and perennial grasses in winter.	Canopy removal by fire yields increased productivity of undergrowth and makes available more open habitat. Fire may retard successional advance of alpine grasslands and improve productivity and palatability of important forage species. Fire can improve nutrition in mountain shrublands by increasing availability of green grass.

(con.)

Table 4 (Con.)

Species	Fire Groups	Habitat considerations	Fire effects
Woodland caribou <i>Rangifer caribou</i>	7,8,9,10,11	Lightly stocked seral or mature spruce-fir forests interspersed with lakes, bogs, and fens provide prime habitat. Lichens are important winter food; shrubs and forbs used during the summer.	Severe stand-replacing fires result in displacement or elimination of caribou use and replacement by moose.
CAUDATA (salamanders)			
Tiger salamander <i>Ambystoma tigrinum</i>	2,4,5,6,7,8, 9,10,11	Found in and near pools, ponds, lakes, and streams. Adults sometimes burrow in decayed logs in damp forest situations.	Impervious to fire except for minor direct mortality in severe fire situations.
Rough-skinned newt <i>Taricha granulosa</i>	11	Inhabits grassland, woodland, and forest in cold permanent streams. Some hide under slabs of bark, logs, or rotten wood in riparian zones.	Generally impervious to fire. Some direct mortality possible in severe fire situations.
Coeur d'Alene salamander (Van Dyke's salamander) <i>Plethodon vandykei</i>	7,8,9,10	Inhabits humid Douglas-fir and dwarf maple forests, in rock and dirt talus and gravel.	Moisture conditions in preferred habitat generally preclude severe fire effects. Habitat destruction by mechanical means has made this species rare.
SALIENTIA (frogs and toads)			
Tailed frog <i>Ascaphus truei</i>	2,4,5,6,7,8, 9	Inhabits cold streams in humid forests of Douglas-fir, spruce, pine, and maple. Comes to shore only on cold rainy days.	Impervious to fire.
Spotted frog <i>Rana pretiosa</i>	2,4,5,6,7,8, 9	Highly aquatic.	Impervious to fire.
Leopard frog <i>R. pipiens</i>	Wide range	Stays around water. In summer it inhabits swamps, grassy woodland, or short-grass meadows.	Generally impervious to fire. Some direct mortality possible from fast-spreading surface fire.
Pacific tree frog <i>Hyla regilla</i>	2,4,5,6,7,8, 9,10,11	Varied habitats. May inhabit damp recesses among rocks and logs in damp woodland or forest. Uses downed logs for hiding and thermal.	Damp habitat minimizes fire effects. Surface fire under severe drying conditions could degrade habitat.
Boreal toad (western toad) <i>Bufo boreas</i>	2,4,5,6,7,8, 9,10,11	Found in or near water. Burrows in loose soil.	Relatively impervious to fire.
CHELONIA (turtles)			
Snapping turtle <i>Chelydra serpentina</i>		Highly aquatic.	Impervious to fire.
Painted turtle <i>Chrysemys picta</i>		Highly aquatic. Basks near the water on mudbanks, rocks, and logs.	Impervious to fire.
SQUAMATA (snakes and lizards)			
Western skink <i>Eumeces skiltonianus</i>	2,4,5,6,7,11	Found in woodland and forest with dense vegetation. Inhabits rocky streamsides, dry grassy hillsides, forest openings, and meadows. Hides under logs and bark. Diet includes moths, beetles, crickets, grasshoppers, and spiders.	Severe surface fires will reduce cover and food supply.
Northern alligator lizard <i>Gerrhonotus coeruleus</i>	2,4,5,6,7,11	Inhabits woodland and forests. Occurs under bark, inside rotten logs, and under rocks and debris. Searches under surface objects for insects and small animals.	Surface fires can destroy habitat and result in some direct mortality.
Rubber boa (Rocky Mountain boa) <i>Charina bottae</i>	2,4,5,6,7,8, 9,10,11	Found near streams and meadows in all forest types; prefers pole to mature stands. Uses rotting logs and bark of fallen and standing dead trees for hiding. Feeds on rodents, insects, and lizards on forest floor.	Severe surface fire can remove cover and temporarily reduce abundance of prey species.

(con.)

Table 4 (Con.)

Species	Fire Groups	Habitat considerations	Fire effects
Racer (Western yellow-bellied racer) <i>Coluber constrictor</i>	2	Inhabits open woodlands, wooded ravines, and thickets. Diet includes lizards, frogs, small rodents, snakes, and insects.	Surface fire may adversely affect food supply.
Gopher snake (bullsnake) <i>Pituophis melanoleucus</i>	2,4,5,6,7	Highly adaptable species; occupies a variety of habitats. Mainly hunts on surface for small mammals.	Relatively impervious to fire because of wide ecological amplitude.
Common garter snake (red-sided garter snake; valley garter snake) <i>Thamnophis sirtalis</i>	2,4,5,6,7,8, 9	Widely distributed in many different habitats that include a water source. Diet largely aquatic but includes small mammals.	Impervious to fire.
Western rattlesnake (prairie rattlesnake) <i>Crotalus viridis</i>	Widespread	Highly variable habitats, including open woodlands to mountain forests. Often found in rock outcrops. Hunts on surface for rodents.	Relatively impervious to fire except for possible direct mortality in severe surface fire situations.

Hypothesized fire tolerance for some western Montana bird species is classified in table 5.

Table 5—Hypothesized fire tolerance for some western Montana birds (adopted from Kramp and others 1983)¹

Fire intolerant	Fire impervious	Fire adapted	Fire dependent
Ash-throated flycatcher (<i>Myiarchus cinerascens</i>)	American crow (<i>Corvus brachyrhynchos</i>)	American kestrel (<i>Falco sparverius</i>)	Blue grouse (<i>Dendragapus obscurus</i>)
Black-capped chickadee (<i>Parus atricapillus</i>)	American robin (<i>Turdus migratorius</i>)	American robin (<i>Turdus migratorius</i>)	House wren (<i>Troglodytes aedon</i>)
Brewer's sparrow (<i>Spizella breweri</i>)	Black-billed magpie (<i>Pica pica</i>)	Black-headed grosbeak (<i>Pheucticus melanocephalus</i>)	Mourning dove (<i>Zenaida macroura</i>)
Brown creeper (<i>Certhia americana</i>)	Blue jay (<i>Cyanocitta cristata</i>)	Blue-winged teal (<i>Anas discors</i>)	Sandhill crane (<i>Grus canadensis</i>)
Burrowing owl (<i>Athene cunicularia</i>)	Blue-winged teal (<i>Anas discors</i>)	Brewer's sparrow (<i>Spizella breweri</i>)	Wild turkey (<i>Meleagris gallopavo</i>)
Cassin's finch (<i>Carpodacus cassinii</i>)	Brown-headed cowbird (<i>Molothrus ater</i>)	Canada goose (<i>Branta canadensis</i>)	
Chipping sparrow (<i>Spizella passerina</i>)	Brown thrasher (<i>Toxostoma rufum</i>)	Clark's nutcracker (<i>Nucifraga columbiana</i>)	
Golden-crowned kinglet (<i>Regulus satrapa</i>)	Canada goose (<i>Branta canadensis</i>)	Cliff swallow (<i>Hirundo pyrrhonota</i>)	
Great horned owl (<i>Bubo virginianus</i>)	Cedar waxwing (<i>Bombycilla cedrorum</i>)	Common nighthawk (<i>Chordeiles minor</i>)	
Hammond's flycatcher (<i>Empidonax hammondi</i>)	Clark's nutcracker (<i>Nucifraga columbiana</i>)	Common poorwill (<i>Phalaenoptilus nuttallii</i>)	
Hermit thrush (<i>Catharus guttatus</i>)	Cliff swallow (<i>Hirundo pyrrhonota</i>)	Cooper's hawk (<i>Accipiter cooperii</i>)	
Mountain chickadee (<i>Parus gambeli</i>)	Common raven (<i>Corvus corax</i>)	Downy woodpecker (<i>Picoides pubescens</i>)	
Northern goshawk (<i>Accipiter gentilis</i>)	Common snipe (<i>Gallinago gallinago</i>)	Fox sparrow (<i>Passerella iliaca</i>)	
Pine siskin (<i>Carduelis pinus</i>)	Eastern kingbird (<i>Tyrannus tyrannus</i>)	Gadwall (<i>Anas strepera</i>)	
Purple finch (<i>Carpodacus purpureus</i>)	European starling (<i>Sturnus vulgaris</i>)	Green-tailed towhee (<i>Pipilo chlorura</i>)	
Pygmy nuthatch (<i>Sitta pygmaea</i>)	Gadwall (<i>Anas strepera</i>)	Hairy woodpecker (<i>Picoides villosus</i>)	
Red-breasted nuthatch (<i>Sitta canadensis</i>)	Great blue heron (<i>Ardea herodias</i>)	House wren (<i>Troglodytes aedon</i>)	

(con.)

Table 5 (Con.)

Fire intolerant	Fire impervious	Fire adapted	Fire dependent
Red crossbill (<i>Loxia curvirostra</i>)	Horned lark (<i>Eremophila alpestris</i>)	Killdeer (<i>Charadrius vociferus</i>)	
Ruby-crowned kinglet (<i>Regulus calendula</i>)	MacGillivray's warbler (<i>Oporornis tolmiei</i>)	Lark sparrow (<i>Chondestes grammacus</i>)	
Rufous-sided towhee (<i>Pipilo erythrophthalmus</i>)	Mallard (<i>Anas platyrhynchos</i>)	Luzuli bunting (<i>Passerina amoena</i>)	
Sharp-shinned hawk (<i>Accipiter striatus</i>)	Mourning dove (<i>Zenaida macroura</i>)	Mallard (<i>Anas platyrhynchos</i>)	
Solitary vireo (<i>Vireo solitarius</i>)	Northern flicker (<i>Colaptes auratus</i>)	Mountain bluebird (<i>Sialia currucoides</i>)	
Western flycatcher (<i>Empidonax difficilis</i>)	Northern pintail (<i>Anas acuta</i>)	Northern flicker (<i>Colaptes auratus</i>)	
Western tanager (<i>Piranga ludoviciana</i>)	Red-winged blackbird (<i>Agelaius phoeniceus</i>)	Northern pintail (<i>Anas acuta</i>)	
White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	Snowy egret (<i>Egretta thula</i>)	Purple martin (<i>Progne subis</i>)	
White-throated sparrow (<i>Zonotrichia albicollis</i>)	Song sparrow (<i>Melospiza melodia</i>)	Red-naped sapsucker (<i>Sphyrapicus nuchalis</i>)	
Yellow-rumped warbler (<i>Dendroica coronata</i>)	Steller's jay (<i>Cyanocitta stelleri</i>)	Rufous-sided towhee (<i>Pipilo erythrophthalmus</i>)	
Yellow warbler (<i>Dendroica petechia</i>)	Townsend's solitaire (<i>Myadestes townsendi</i>)	Snowy egret (<i>Egretta thula</i>)	
	Turkey vulture (<i>Cathartes aura</i>)	Three-toed woodpecker (<i>Picoides tridactylus</i>)	
		Tree swallow (<i>Tachycineta bicolor</i>)	
		Vaux's swift (<i>Chaetura vauxi</i>)	
		Vesper sparrow (<i>Pooecetes gramineus</i>)	
		Violet-green swallow (<i>Tachycineta thalassina</i>)	
		Western bluebird (<i>Sialia mexicana</i>)	
		Western kingbird (<i>Tyrannus verticalis</i>)	
		Western meadowlark (<i>Sturnella neglecta</i>)	
		Western screech owl (<i>Otus kennicottii</i>)	
		Western wood-pewee (<i>Contopus sordidulus</i>)	
		Wild turkey (<i>Meleagris galopavo</i>)	
		Williamson's sapsucker (<i>Sphyrapicus thyroideus</i>)	
		Winter wren (<i>Troglodytes troglodytes</i>)	

¹Scientific and common names follow the American Ornithologists' Union (A.O.U.) 1983 Check-list as contained in the National Geographic Society, **Field Guide to the Birds of North America**, 1983. 464 p.

SUMMARY ON DOWNED, DEAD FUEL

Downed dead woody fuel consists of dead twigs, branches, stems, and boles of trees that have fallen and lie on or near the ground (Brown and See 1981). Table 6 is a summary of such fuel for western Montana forests based on 6 years of Forest Service forestwide inventories on the Bitterroot, Flathead, Kootenai, and Lolo National Forests. These inventories were conducted for timber management planning, often in anticipation of timber harvest, so many stands were "high risk" stands with higher than normal

fuel accumulations. Fuel loads and duff depths are presented in table 6 for seven different habitat type groups defined by Brown and See (1981) based on similarity of loading and correspondence to the habitat type Fire Groups.

The values in table 6 are group averages. Habitat type averages are shown in figure 3, which also shows how habitat type loadings compare. Brown and See (1981) provide additional summaries of fuel loads that should be useful aids for fire management.

Table 6—Average downed woody loadings and duff depths for western Montana forests by habitat type, loading groups, and equivalent Fire Groups (source: Brown and See 1981)

Habitat type loading groups ¹	Equivalent habitat type Fire Groups	Downed woody				Duff depth
		¹ / ₄ -1 inch	1-3 inches	Over 3 inches	Total woody	
		----- Tons/acre -----				Inches
2	2,3,4,5	0.8	1.5	10.9	13.2	0.9
3	6	.9	1.5	9.1	11.5	1.0
4	7,8	.9	1.5	15.6	18.4	1.1
5	9	.9	1.8	22.0	24.7	1.5
6	10	.8	1.4	15.6	17.8	1.3
7	11	1.3	2.2	21.5	25.0	1.8

¹2 = Dry site Douglas-fir and moist site ponderosa pine.

3 = Moist site Douglas-fir.

4 = Cool sites dominated by lodgepole pine; dry, lower elevation subalpine fir.

5 = Moist site, lower elevation subalpine fir.

6 = Cold, moist site upper elevation subalpine fir.

7 = Warm, moist sites; mostly cedar-hemlock.

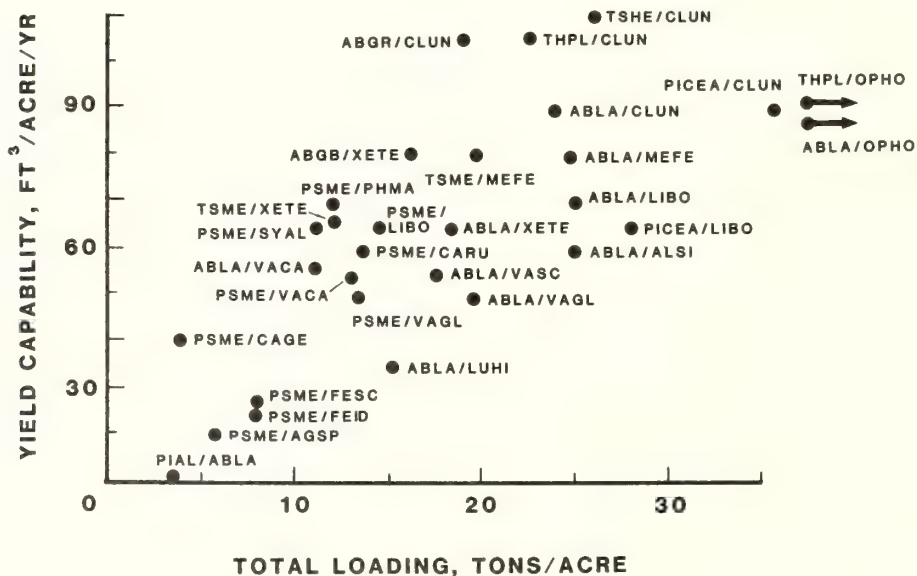


Figure 3—Ordination of habitat types by yield capability and total downed woody fuel loading for western Montana and northern Idaho National Forests. Yield capabilities are from Pfister and others (1977). Plotted habitat types are represented by at least five stands or 35 sample points (source: Brown and See 1981). See table 1 for Fire Group assignment of habitat types.

FIRE USE CONSIDERATIONS

Fire management applications of fire ecology information are presented at the end of each Fire Group discussion. The use of fire to accomplish certain resource management objectives is suggested in these fire management presentations. The following fire use considerations apply generally to all Fire Groups.

Heat Effects and Insect Attack

Care must be taken when burning in forest stands to prevent or minimize scorching the crowns of residual overstory trees. Heavy fuel accumulations or slash concentrated near the base of overstory trees may require scattering or other treatment to avoid lethal cambium heating. Excessive crown scorch, cambium damage, or both can result in loss of vigor and increased susceptibility to bark beetle attack or tree mortality. For example, the relationships between crown defoliation and mortality caused by the western pine beetle in ponderosa pine have been generalized as follows (Stevens and Hall 1960):

Percentage defoliation	Percentage of trees killed by beetles
0-25	0-15
25-50	13-14
50-75	19-42
75-100	45-87

The season in which a fire occurs is an important factor influencing tree mortality and the occurrence, duration, and severity of a potential beetle attack on fire-weakened trees. The result of crown scorching is usually more severe during the active growth period early in the summer than later when growth has slowed, terminal buds have formed, and a food reserve is being accumulated (Wagener 1955, 1961). Likewise, crown scorching that occurs in early spring, before or immediately after bud burst, often results in minimum damage to the tree.

Prescribed burning of understory vegetation and dead surface fuels can be carried out without serious threat of subsequent damage by bark beetles provided the overstory trees are not severely scorched (Fischer 1980). If accidental scorching does occur and bark beetle activity is detected, prompt removal of the severely scorched trees will reduce the probability of subsequent damage to healthy green trees. If scorching occurs outside the active growth period, scorched trees may recover and regain lost vigor. This may take 3 years, but signs of recovery should be visible during the first growing season that follows scorching.

Frequency of Burning

The effects of repeated burning on a given site are not well defined for western Montana forests. Consequently, it seems prudent to gear the frequency of prescribed fire on a site to the wildfire frequencies that existed prior to organized fire suppression (see Arno 1980). Consequences of too frequent fire might include loss of seed source, loss of nutrients, and a decline in the fertility of the site.

Large Woody Debris

An important fire use consideration is the need to retain a certain amount of woody material for maintenance of forest site quality. Current understanding of the relationships between organic matter and ectomycorrhizae in Northern Rocky Mountain forest soils is based on work by Harvey, Jurgensen, and Larsen in western Montana (Harvey 1982). They found ectomycorrhizal development was stimulated by the presence of decayed wood in the soil. Decayed wood also has a moisture and nutrient regime often favorable to continued seedling growth. These potential benefits are especially important on moderately dry sites.

Scattered large logs left on a site also retard soil movement and provide shade for young seedlings. The more tolerant tree species such as subalpine fir or Engelmann spruce will not successfully regenerate without at least partial shade. Harvey and others (1981) suggest that about 11 to 17 tons per acre (2.5 to 3.8 kg/m²) of fresh residues larger than 6 inches (15 cm) in diameter should be left on the site following logging and burning. In addition, only as much mineral soil should be bared as is necessary to obtain desired stocking. These authors further suggest that amounts of organic matter in excess of the above requirements can be considered undesirable especially on dry sites. Excess buildup of fuels can set the stage for high-intensity wildfires that result in an extreme reduction of the soil's organic reserves. Numerical relationships for predicting duff and woody fuel consumption by prescribed fire in the Northern Rocky Mountains are provided by Brown and others (1985).

A final reason for leaving moderate amounts of large diameter woody debris scattered on the site following logging and burning is to supply food and cover for wildlife. Many small mammals that reside in western Montana forests rely on forest floor debris for cover and nesting sites. Rotten logs are often important foraging sites for both mammals and birds. Logs, for example, are important feeding sites for pileated woodpeckers.

Woodpeckers and other cavity-nesting birds (and mammals) also require snags, preferably scattered patches of snags, for nesting sites (McClelland and Frissell 1975; McClelland and others 1979).

The need to retain moderate amounts of scattered large-diameter woody debris should not preclude slash disposal. Unabated logging slash represents a significant fire hazard on most sites, usually greatly in excess of the pretreatment situation. This increased hazard will exist for at least 3 to 5 years, even with a maximum compaction effect from winter snows.

Unabated logging slash as well as large accumulations of deadfall in untreated stands can affect elk behavior and movement. Elk use may be diminished when slash inside a treatment unit exceeds 1.5 ft (0.5 m) in depth and dead and down material outside the opening exceeds 1.5 ft (0.5 m) (Boss and others 1983).

Heat Effects on Soil

Properly applied, prescribed fire has a low risk of causing long-term adverse effects on the fertility of the most common western Montana soils. However, the effect on

naturally infertile soils is unclear and should be monitored. The intense heat and ashes resulting from burning dozer-piled slash can affect regeneration success on the area occupied by the piles. Therefore, size of piles should be kept small, and burning should be deferred to periods of relatively high fuel and soil moisture (Holdorf 1982).

Prescribed Fire Planning

From a fire management perspective, a successful prescribed fire is one that is executed safely, burns under control, accomplishes the prescribed treatment, and attains the land and resource management objectives for the area involved. Successful prescribed burning requires planning. Such planning should be based on the following factors (Fischer 1978):

1. Physical and biological characteristics of the site to be treated.
2. Land and resource management objectives for the site to be treated.
3. Known relationships between preburn environmental factors, expected fire behavior, and probable fire effects.
4. The existing art and science of applying fire to a site.
5. Previous experience from similar treatments on similar sites.

FIRE GROUP ZERO: MISCELLANEOUS SPECIAL HABITATS

Group Zero is a miscellaneous collection of habitats that do not fit into the Montana habitat type classifications.

Scree

Scree refers to slopes covered with loose rock fragments, usually lying near the maximum possible angle of repose so that any disturbance causes minor rock slides down the face of the slope. Scree slopes may be treeless or they may support scattered trees with sparse undergrowth. Usually scree communities are regarded as special environments where the vegetation is in an uneasy equilibrium with the unstable substrate.

The discontinuous fuel often makes scree slopes unburnable. Individual trees or islands of vegetation may ignite, but fire spread is limited. A severe wind-driven fire could pass over the intervening open spaces and destroy a scree community, but this rarely happens. Due to the harsh environment, these sites do not revegetate well, and revegetation following a fire can take a long time.

Forested Rock

Forested rock is usually a steep canyon wall or mountainside composed of rock outcrops, cliffs, and occasional clumps of trees clinging to ledges and crevices. Species growing here include ponderosa pine, Douglas-fir, juniper, and alder. Forested rock is especially prominent along the canyons of major rivers and in rugged upper subalpine areas near timberline. These sites bear a certain similarity to scree sites, but the substrate is solid and climax species frequently become established.

Surface fires do not burn well because of the vertical and horizontal discontinuity of ground fuels. The probab-

ity of crown fires depends on the density and arrangement of trees on the rock face. In some cases the islands of vegetation are so widely scattered as to be almost immune to wildfire. In other cases, particularly low-elevation Douglas-fir forested rock communities, a continuity of foliage from the base to the top of a cliff can occur. Each tree forms a ladder into the lower branches of the next higher tree upslope. In such cases crown fires can occur over ground that would not support a less severe surface fire.

Revegetation of rocky sites proceeds at a rate characteristic of the site and depends on the severity of the fire, the age and depth of the soil on ledges and in pockets of rock, erosion if any, and the availability of seeds.

Wet Meadow

A meadow is an opening in the forest that is characterized by herbaceous vegetation and abundant water. Subirrigation is common during at least some part of the growing season. Mountain meadows are frequently too wet to burn during the fire season. In midsummer, wet meadows often act as natural firebreaks, but during the late summer and early fall they may carry grass fires. In some situations, especially when meadows are dominated by grass, they may burn early in the spring following snowmelt and prior to greenup.

Streamside meadows may gradually become drier in the course of succession from a hydric to a mesic condition. The buildup of organic material and trapped sediments from the flowing water, combined with a possible deepening of the streambed and lowering of the water table, can leave former meadows in an intermediate condition between wet meadow and grassland. In some such sites the meadow becomes bordered by fire-maintained grassland. Fire suppression has allowed conifers to invade meadows where they would not normally be found.

Mountain Grassland

A mountain grassland (or grassy bald) is a grass-covered opening within an otherwise continuous coniferous forest. Mountain grasslands may act as firebreaks and can be maintained as grassland by light fires, but usually their fire ecology is less obvious. Despain (1973) found boundaries between grassland and forest in the Bighorn Mountains of Wyoming, which he attributed to topography and soils. Daubenmire (1943) suggested that soil factors might cause permanent mountain grasslands. It is also possible that these are natural grasslands that have little potential for forest development. Caution is indicated in management of stands adjacent to mountain grasslands until conditions responsible for their perpetuation are determined.

Aspen Grove

Groves of quaking aspen or quaking aspen and black cottonwood can occur as local climax vegetation on streamside sites or as fire-maintained stands in areas that would otherwise be dominated by conifers. In the fire-maintained areas, the absence of fire can result in the gradual elimination of aspen due to lack of successful regeneration by suckering.

Alder Glade

An alder glade is an opening in the forest occupied by alder. Such sites usually appear on local areas that are too wet for associated conifers. Because they are wet, alder glades burn infrequently, but they can burn intensely and then resprout from surviving underground stems. Burning tends to make the stand more dense because each burned plant puts up several new shoots during recovery. Alder, like aspen, can exist as a fire-maintained stand in areas where conifer invasion is possible.

Fire Management Considerations

Group Zero sites will not burn readily under normal summertime weather conditions. Fire managers can take advantage of this fact when developing preattack plans and when delineating fire management areas, units, or zones. These sites can also serve as anchor points for fuelbreaks and firebreaks.

Meadows and aspen groves can be important wildlife habitats. Prescribed fire is a suitable tool for maintaining desired forage conditions on these sites.

FIRE GROUP TWO: WARM, DRY PONDEROSA PINE HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
130	<i>Pinus ponderosa</i> / <i>Agropyron spicatum</i> h.t. (PIPO/AGSP), ponderosa pine/bluebunch wheatgrass	Northwestern and west central
141	<i>Pinus ponderosa</i> / <i>Festuca idahoensis</i> h.t.- <i>Festuca idahoensis</i> phase (PIPO/FEID-FEID), ponderosa pine/Idaho fescue-Idaho fescue phase	West central
142	<i>Pinus ponderosa</i> / <i>Festuca idahoensis</i> h.t.- <i>Festuca scabrella</i> phase (PIPO/FEID-FESC), ponderosa pine/Idaho fescue-rough fescue phase	West central
161	<i>Pinus ponderosa</i> / <i>Purshia tridentata</i> h.t.- <i>Agropyron spicatum</i> phase (PIPO/PUTR-AGSP), ponderosa pine/antelope bitterbrush/bluebunch wheatgrass phase	West central
162	<i>Pinus ponderosa</i> / <i>Purshia tridentata</i> h.t.- <i>Festuca idahoensis</i> phase (PIPO/PUTR-FEID), ponderosa pine/antelope bitterbrush-Idaho fescue phase	Northwestern and west central
171	<i>Pinus ponderosa</i> / <i>Symphoricarpos albus</i> h.t.- <i>Symphoricarpos albus</i> phase (PIPO/SYAL-SYAL), ponderosa pine/common snowberry-common snowberry phase	Northwestern and west central

Vegetation

Fire Group Two consists of ponderosa pine stands with predominantly grass undergrowth. These sites may exist as fire-maintained grassland and will support Rocky Mountain juniper and Douglas-fir as accidental individuals. Rocky Mountain juniper may be a minor climax species on some sites. Sites are typically hot, dry, south-facing and west-facing slopes at low elevations, forming the lower timberline in the area. Slopes are often steep with poorly developed soils. Moisture stress is a critical factor for plant growth during summer months. Stocking limitations often result in low productivity, although some sites regenerate readily.

In the undergrowth, common snowberry, antelope bitterbrush, and chokecherry are important shrubs. On rocky outcrops near Darby, MT (Bitterroot National Forest), curleaf mountain-mahogany (curleaf cercocarpus) is common. Herbaceous species include Idaho and rough fescue and white stoneseed.

Forest Fuels

Fuel loads tend to be light when compared to other Fire Groups. Often, the most abundant surface fuel is cured grass. This is especially true for mature, open-grown stands of ponderosa pine. Downed woody fuels in such stands usually consist of widely scattered, large trees (deadfalls) and concentrations of needles, twigs, branchwood, bark flakes, and cones near the base of individual trees. Fuel loads in such stands may be less than 1 ton per acre (0.2 kg/m²).

Fuel loads in dense pole and small sawtimber stands may be much higher than in the older open-type stands. Figure 4 and table 7 show a range of loadings that can exist in these young stands.

Role of Fire

The natural role of fire in warm, dry ponderosa pine stands is threefold:

1. To maintain grasslands. Grassland areas capable of supporting juniper and ponderosa pine may remain treeless through frequent burning.
2. To maintain open ponderosa pine stands. The open condition is perpetuated by periodic fires that either reduce the number of seedlings, remove dense understories of sapling or pole-sized trees, or thin overstory trees.
3. To encourage ponderosa pine regeneration. Fire exposes mineral soil, reduces seedling-damaging cutworm populations, reduces competing vegetation, and increases nutrient availability. Depending on the subsequent seed crop, weather, and continuity of the seedbed, regeneration may appear as dense stands, separated thickets, or scattered individuals. Periodic fires can create uneven-aged stands comprising various even-aged groups. Severe fires will result in a predominantly even-aged stand.

Historically, natural fire frequencies in forests adjacent to grasslands were fairly high, according to numerous studies conducted in the ponderosa pine forest types throughout the Western States. These studies show fire to have been a frequent event, at intervals from 5 to 25



Figure 4—A range of Group Two fuel loads: Stand 24 is a 137-year-old ponderosa pine stand on a ponderosa pine/Idaho fescue h.t.-Idaho fescue phase; Stand 72 is an 8-year-old ponderosa pine stand on a ponderosa pine/common snowberry h.t.-common snowberry phase. See table 7 for fuel load by size class, total fuel load, and duff depth.

Table 7—Fuel loadings by size class for stands shown in figure 4

Stand number	Age ¹	Habitat type-phase	Size class (inches)						Total
			0-1/4	1/4-1	1-3	3-6	6-10	10-20	
	Years		Tons/acre						
24	137	PIPO/FEID-FEID	0.10	0.60	0.40	0.10	0	0	1.10
72	80	PIPO/SYAL-SYAL	.14	2.20	4.40	5.34	2.30	2.10	16.48

¹Age is of overstory dominants.

years in most locations. On the Bitterroot National Forest, Arno (1976) and Arno and Peterson (1983) reported a range of 2 to 20 years and mean fire-free intervals of 6 to 12 years for fires somewhere in small stands of 50 to 100 acres (20 to 40 ha). Fire history investigators caution that these figures are conservative estimates of past mean fire-free intervals. Intervening light ground fires could have effects on stand development without leaving scars on trees.

Wright (1978) suggests a fire interval of 50 years or more for the PIPO/PUTR h.t. He bases this hypothesis on observation and current knowledge of the susceptibility of bitterbrush to fire (Nord 1965; Weaver 1967; Wright 1978). Other investigators suggest that ponderosa pine communities with shrub understories experienced fire frequencies of considerably less than 50 years (Gruell and others 1982; Weaver 1957, 1959, 1961).

The effects of fire suppression during the 20th century on some sites have been confounded by the rocky, dry nature, low site productivity, and the influence of grazing.

In more productive sites, the absence of fire has resulted in overstocking and increased fuels. Natural regeneration is often quite slow, and in many cases fire suppression has caused little fuel buildup. In fact, on gravelly south slopes, fuels are light and variable both vertically and horizontally in spite of 50 years or more without fire. Occasionally, thickets of moderate to heavy fuels do occur, but the surrounding sparse fuels and open stand structure tend to reduce the hazard. Such areas may not be available to burn during years of low to moderate fire danger simply because of lack of fuel. However, during severe fire danger, wind-driven fires may spread through the sparse dry fuels.

Forest Succession

A generalized concept of natural forest succession for Fire Group Two sites and how fire affects this succession is shown in figure 5 (subsequent numbers in this section refer to fig. 5).

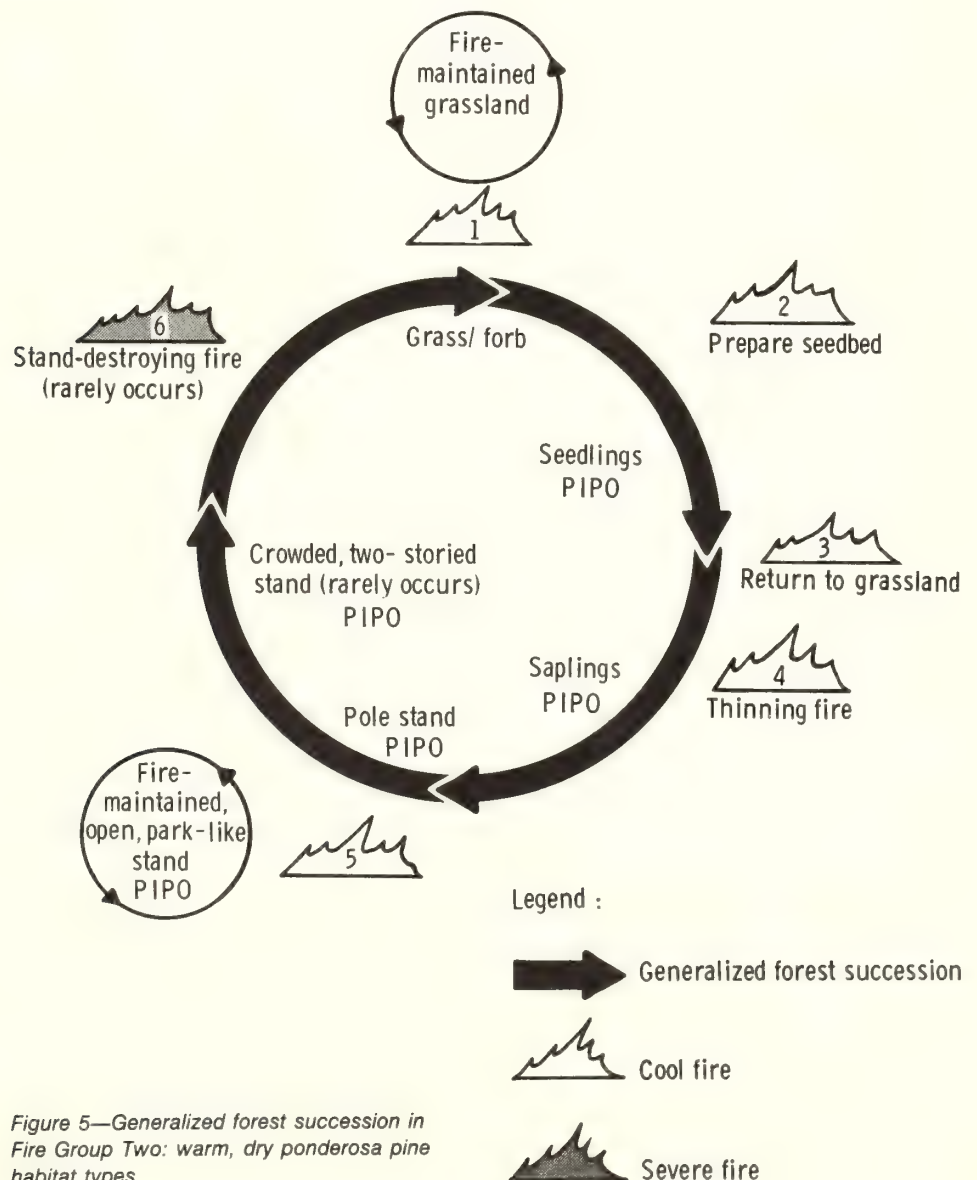


Figure 5—Generalized forest succession in Fire Group Two: warm, dry ponderosa pine habitat types.

Frequent fires tend to maintain the grassland community by killing pine seedlings (No. 1). Grasses dominate the undergrowth, but other herbs and small shrubs may be present. Ponderosa pine seedlings may become established gradually over a long fire-free period resulting in an all-aged, all-sized stand, or as a single age class following a seedbed-preparing fire (No. 2). In the absence of further burning, the seedlings develop into saplings. Fires during this period may have the effect of killing the young trees (No. 3) or thinning them (No. 4).

With sufficient time the remaining saplings mature to pole-sized trees. Subsequent light ground fires tend to produce an open stand of mature trees (No. 5). In the absence of fire, the stand may (in theory) become overstocked and accumulate enough fuel to support a severe stand-destroying fire (No. 6).

Successional pathways that reflect the interaction of fire, the absence of fire, and silvics on forest stand development are hypothesized in figure 6.

Fire Management Considerations

Fire management considerations for Fire Group Two are wildfire hazard reduction, forage production, site preparation and stocking control, and recreation site development and maintenance.

Wildfire Hazard Reduction—Prescribed fire can be used to reduce dense patches of small trees and accumulated dead grass, needles, and woody debris in stands of pole-sized and larger trees, thereby lessening the chance of tree-killing wildfires. Similarly, slash hazard can be reduced by broadcast burning after cutting. Where heavy fuel loads exist prior to the initial entry with prescribed fire, it is often best to plan several burns in successive years rather than to risk the cambium kill and crown scorch often associated with a hot fire. Heavy fuel loads can also be reduced through firewood removals and, during safe periods, piling and burning. Once fuels have been reduced to an acceptable level, periodic light burning can be used to maintain stands in a low-hazard condition.

Forage Production—Within the PIPO/AGSP h.t., PIPO/FEID h.t., and PIPO/SYAL h.t. light surface fires will rejuvenate shrubs through sprouting and cause a temporary increase in grass and forb production. Grazing may have to be deferred for 1 or 2 years before burning on open, heavily grazed sites where percentage of cover by plants is low and litter is sparse. Where it will carry, fire can be used to rejuvenate the undergrowth, especially within the PIPO/PUTR h.t., by killing decadent bitterbrush and thereby regenerating the site from onsite sprouting or from offsite seed cached in the burn by rodents. As a general rule, luxuriant growth of shrubs will not result from fire use on Group Two sites.

Site Preparation and Stocking Control—Fire can create a mineral soil seedbed where this is necessary for successful ponderosa pine regeneration. Once a new stand is established and an adequate number of trees 10 to 12 ft (3 to 3.7 m) or taller are in the overstory, fire can be used to thin the new stand (Wright 1978). Subsequent use of fire at intervals of 5 to 10 or 15 years will remove unnecessary reproduction and accumulated dead woody fuel,

thereby increasing stand vigor, reducing fire hazard, and increasing grass, forb, and shrub production (Wright 1978).

Recreation Site Development and Maintenance—Prescribed fire or partial cutting and prescribed fire can be used to create parklike openings underneath mature stands of ponderosa pine in which campgrounds and picnic areas can be installed. Periodic use of fire in spring or fall can maintain such openings and reduce fire hazard in and around campgrounds.

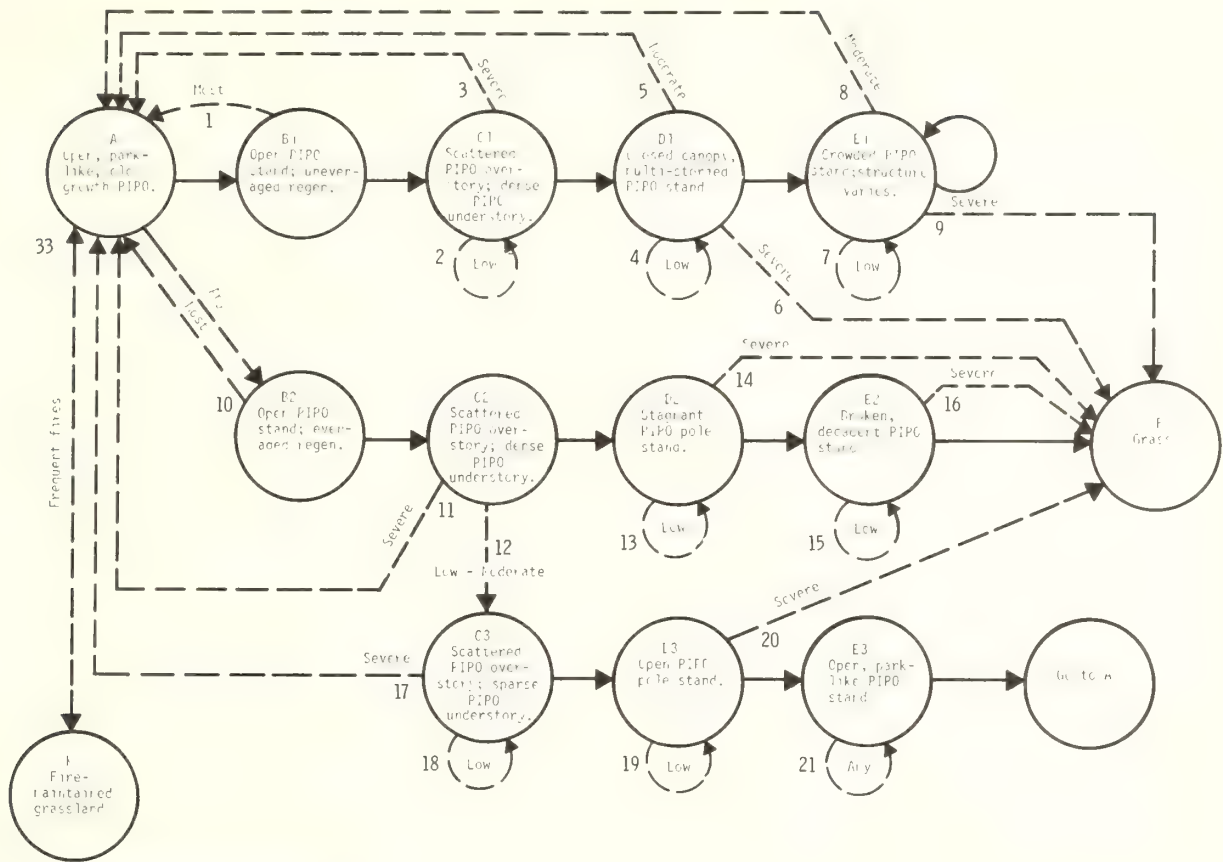
FIRE GROUP FOUR: WARM, DRY DOUGLAS-FIR HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
210	<i>Pseudotsuga menziesii</i> / <i>Agropyron spicatum</i> h.t. (PSME/AGSP), Douglas-fir/bluebunch wheatgrass	Northwestern and west central
230	<i>Pseudotsuga menziesii</i> / <i>Festuca scabrella</i> h.t. (PSME/FESC), Douglas-fir/rough fescue	Northwestern and west central
262	<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> h.t.- <i>Calamagrostis rubescens</i> phase (PSME/PHMA-CARU), Douglas-fir/ninebark-pinegrass phase	Northwestern and west central
311	<i>Pseudotsuga menziesii</i> / <i>Symphoricarpos albus</i> h.t.- <i>Agropyron spicatum</i> phase (PSME/SYAL-AGSP), Douglas-fir/snowberry-bluebunch wheatgrass phase	Northwestern and west central
321	<i>Pseudotsuga menziesii</i> / <i>Calamagrostis rubescens</i> h.t.- <i>Agropyron spicatum</i> phase (PSME/CARU-AGSP), Douglas-fir/pinegrass-bluebunch wheatgrass phase	Northwestern and west central
324	<i>Pseudotsuga menziesii</i> / <i>Calamagrostis rubescens</i> h.t.- <i>Pinus ponderosa</i> phase (PSME/CARU-PIPO), Douglas-fir/pinegrass-ponderosa pine phase	Northwestern and west central
340	<i>Pseudotsuga menziesii</i> / <i>Spiraea betulifolia</i> h.t. (PSME/SPBE), Douglas-fir/white spirea	Northwestern and west central

Vegetation

Group Four consists of Douglas-fir habitat types where ponderosa pine usually occurs as a major seral or climax associate especially at lower elevations. Group Four stands may exist as fire-maintained ponderosa pine stands that develop Douglas-fir regeneration beneath the pine in the

1. SUCCESSION FROM THE OPEN, PARKLIKE, OLD GROWTH PONDEROSA PINE STATE



2. SUCCESSION FROM THE GRASS STATE

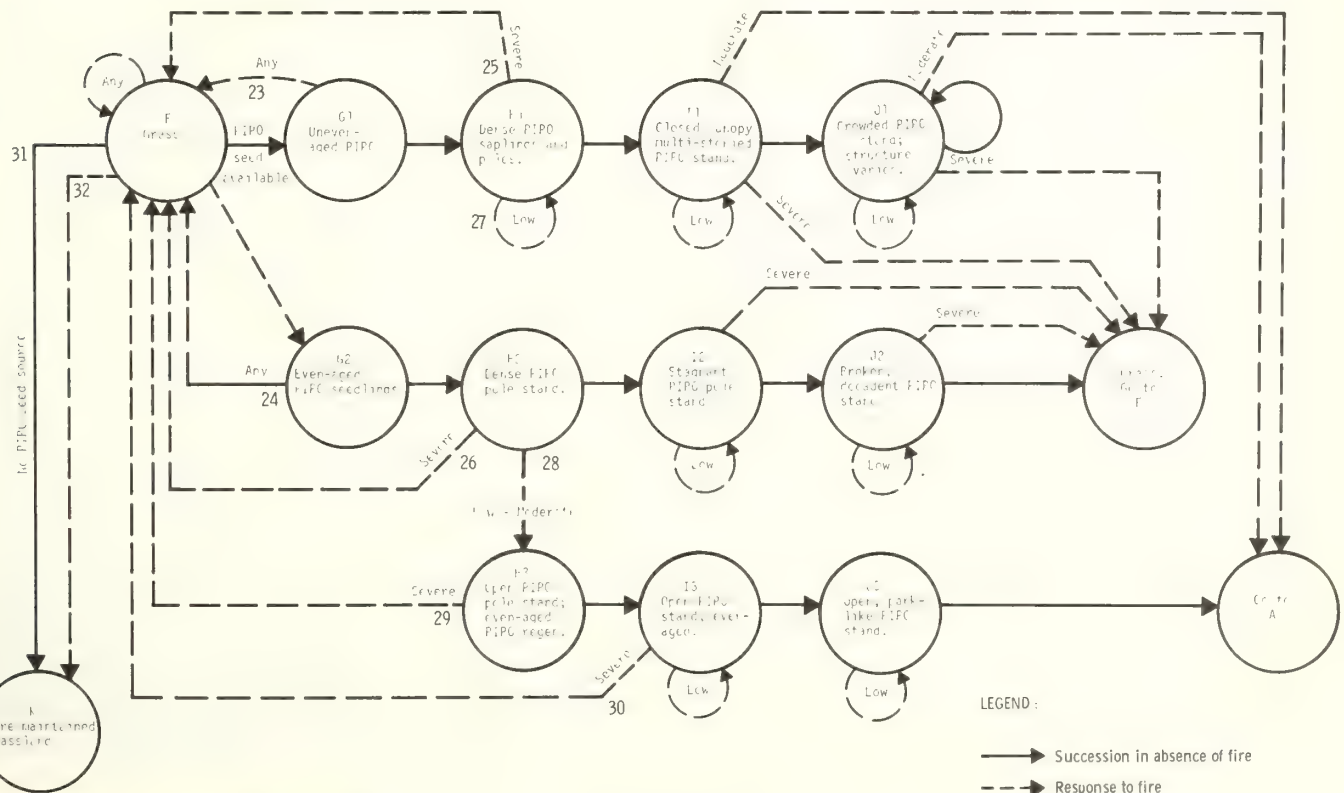


Figure 6—Hypothetical fire-related successional pathways for Fire Group Two habitat types. (1) Succession from the open, parklike, old-growth ponderosa pine state and (2) succession from the grass state.

absence of disturbance. Douglas-fir is usually present in seral stands, but ponderosa pine often dominates. Sites are too droughty for most other conifer species.

Rocky Mountain juniper may be a minor climax species within the PSME/AGSP h.t. Stands tend to be open, but dense stands or thickets can occur in the absence of fire or where good seed years and favorable moisture conditions have followed fire. The understory is usually sparse because of lack of moisture. Major herbs include bluebunch wheatgrass, rough and Idaho fescue, pinegrass, arrowleaf balsamroot, white stoneseed, junegrass, and spreading dogbane. The most common shrubs are common snowberry, kinnikinnick, white spirea, chokecherry, western serviceberry, and mountain ninebark.

Forest Fuels

Fuel loads are heavier on the average than those found in Fire Group Two ponderosa pine stands but lighter than those in most other groups. The average fuel load for the stands that were sampled was about 11 tons per acre (2.5 kg/m²). As a general rule, fuel loads tend to increase with the stand age as a result of accumulated downfall from insect and disease damage, blowdown, and natural thinning. This is especially true in dense, young stands where heavy mortality from natural thinning (suppression mortality) can cause rapid fuel accumulation.

The different types of fuel situations likely to be encountered are shown in figure 7 and listed in table 8. All of these ponderosa pine stands are growing within a PSME/PHMA-CARU h.t.

Stand 73 (fig. 7) is a ponderosa pine stand that represents the average fuel load for the group. Most of the downed, dead fuel is the result of accumulated downfall of material larger than 3 inches (7.6 cm) in diameter (table 8).

The relationship between stand condition and fuel load is suggested by stands 76 and 75 (fig. 7). Both stands are 60-year-old ponderosa pine stands within a PSME/PHMA-CARU h.t. These stands are growing within 0.5 mile (0.8 km) of each other in the same drainage. Downfall from natural thinning is responsible for the considerable difference in fuel loads (table 8).

Sometimes the combined effect of moderate amounts of periodic deadfall and moderate amounts of natural downfall from natural thinning will result in a heavy fuel load. This is shown in stand 74 (fig. 7).

Live fuels can be a significant factor in some Group Four stands. Dense thickets of Douglas-fir regeneration may become established during fire-free periods. Overstories become susceptible to stand-destroying crown fire when such situations are allowed to develop.

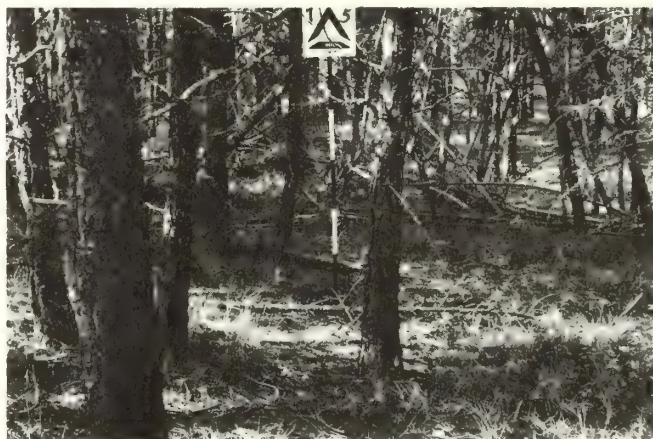


Figure 7—Examples of Group Four fuel loads on the Douglas-fir/mountain ninebark h.t.-pinegrass phase. Stand age, total fuel load, and fuel load by size class are given in table 8.

Table 8—Fuel loadings by size class for stands shown in figure 7

Stand number	Habitat type-phase	Age ¹	Duff depth	Size class (inches)								Total
				0-1/4	1/4-1	1-3	3-6	6-10	10-20	20 +		
				Years	Inches	Tons/acre						
76	PSME/PHMA-CARU	60		0.1	0.9	0.8	0.6	0.1	0	0	2.5	
75	PSME/PHMA-CARU	65		.5	1.4	4.6	3.1	.5	.7	0	10.8	
73	PSME/PHMA-CARU	175		.5	1.0	1.1	1.8	5.6	1.5	0	11.5	
74	PSME/PHMA-CARU	175		.9	1.7	3.6	4.0	4.5	1.8	3.7	20.2	

¹Age is of overstory dominants.

Role of Fire

In the Douglas-fir climax series habitat types, naturally occurring fire will maintain grasslands, open stands of Douglas-fir or seral ponderosa pine, and prepare seedbeds (see Group Two). But there are additional effects (Davis and others 1980):

- 1. Frequent fires in seral stands maintained a ponderosa pine “fire climax” condition by killing fire-susceptible Douglas-fir seedlings. In this role, fire frequency largely determined the stand composition.
- 2. Following a prolonged fire-free period, Douglas-fir regeneration became established beneath the canopy. A ground or surface fire that reached a thicket of saplings and small poles could ascend into the overstory, killing or injuring adjacent mature trees through the vegetative “fuel ladder.” Fuel ladders increased the potential destructiveness of a fire by providing access to the canopy. During periods of high fire danger, this often resulted in a stand-destroying crown fire.

Historic fire frequency probably was not different from that of Group Two—usually 5 to 25 years between fires. Successful suppression of surface fires in open, fire-

maintained stands over the last several decades has increased the potential for a fire to become severe.

Forest Succession

The theoretical climax forest is an all-aged or multi-storied Douglas-fir forest, as shown in figure 8 (subsequent numbers in this section refer to fig. 8). Such a forest is unlikely to be achieved because of the prolonged fire-free period necessary for its development. Most old-growth forests will be open stands with varying under-stories depending on the stand’s fire history. A grass/forb community with shrubs and conifer seedlings becomes established following a severe stand-destroying fire (No. 1). Frequent fire during this stage can result in a fire-maintained grassland (No. 2). A light burn during the herb/shrub stage may result in a seedbed favorable to conifer seedlings, but this may be unimportant where seedling establishment is not hindered by ground cover.

In the absence of fire, the herb/shrub stage gives way to conifer seedlings. Except on those high-elevation sites above its cold limits, ponderosa pine will dominate initially if it dominated the prefire stand. Douglas-fir seedlings will

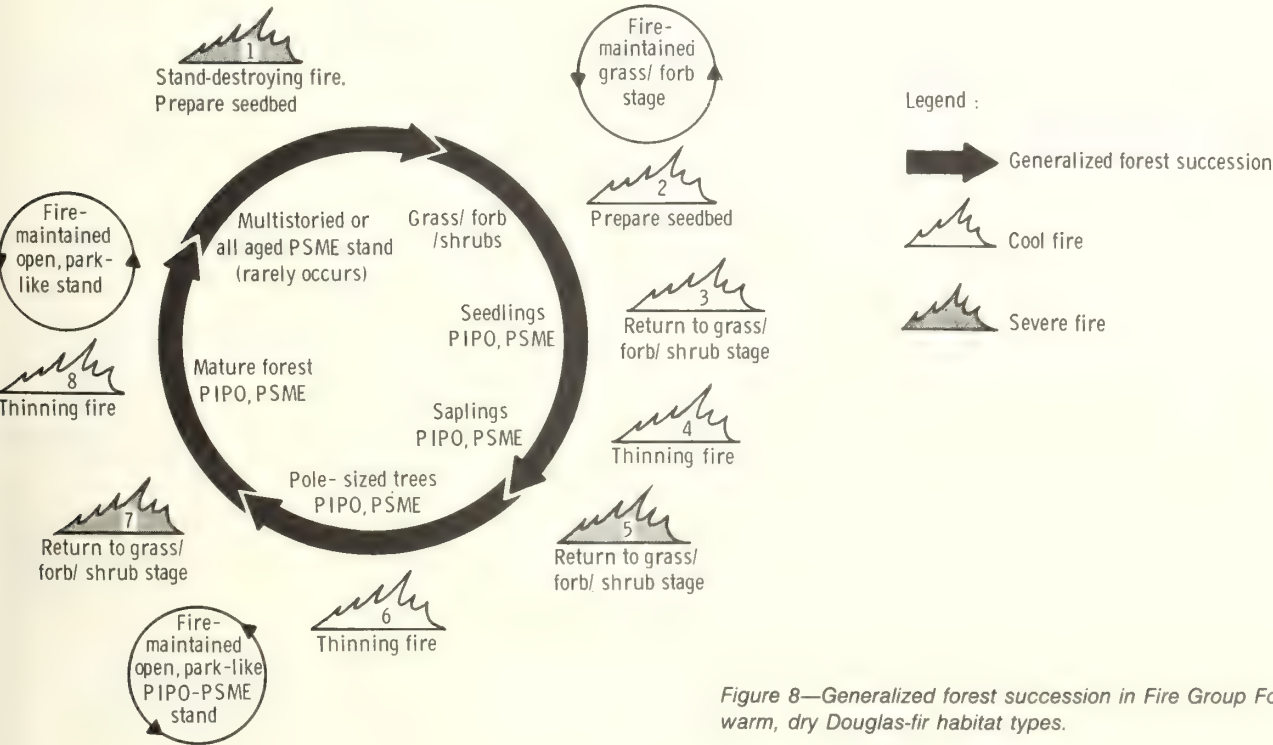


Figure 8—Generalized forest succession in Fire Group Four: warm, dry Douglas-fir habitat types.

also be present. Variation in seed crops is a factor in regeneration. A poor seed year often retards regeneration. A fire at this stage reverts the site to an herb/shrub state (No. 3).

In the absence of fire, ponderosa pine and Douglas-fir saplings develop. Species composition and density of stems depends on site conditions, length of the regeneration period, and how long fire has been absent. Not much ponderosa pine, for example, will be present if fire is absent for a prolonged period. A severe fire returns the site to the herb/shrub stage (No. 5). A light to moderate severity fire tends to thin out Douglas-fir saplings and badly suppressed ponderosa pine saplings (No. 4). A cool fire at this stage will also remove any recent seedlings.

The pole-sized tree stage can be represented by (1) a rather open stand of Douglas-fir and ponderosa pine poles with a scattered seedling and sapling understory, (2) a predominantly ponderosa pine or Douglas-fir pole stand with varying understory, or (3) a scattered pole stand with grass/forb/shrub understory. A light to moderately severe fire at this stage may thin the stand, removing understory vegetation and susceptible Douglas-fir stems (No. 6). Frequent fire maintains an open, parklike stand of ponderosa pine on most sites. A severe fire reverts the site to the herb/shrub state (No. 7).

A mature forest of ponderosa pine, Douglas-fir, or a combination of the two, will eventually develop. Periodic fire at this stage maintains the stand in an open, parklike condition (No. 8). Douglas-fir and some ponderosa pine regeneration may form in the understory of such stands during fire-free intervals. If fire is excluded for an unusually long period, the theoretical climax situation could develop.

Hypothetical succession following fire and the absence of fire in this group is presented in figure 9. The elevation and geographic location of the site is a major determinant of species composition. Ponderosa pine will play a major role in plant succession on most Group Four sites.

The successional sequences of community types and accompanying information provided by Arno and others (1985) can be used to aid predictions of successional development of seral communities (and treatment response) within the PSME/PHMA-CARU h.t.'s in relation to various fire and harvest treatments.

Fire Management Considerations

For Group Four, fire management considerations include wildfire hazard reduction, silviculture, range and wildlife habitat management, and recreation and esthetics.

Wildfire Hazard Reduction—In the prolonged absence of fire and fuel management, hazardous fuel situations often develop. The combination of dense Douglas-fir (or ponderosa pine) understories, accumulated deadfall, decadent shrubs, and other accumulated litter and debris can produce fires severe enough to scorch the crowns and kill the cambium of overstory trees. Guidelines provided by Brown and others (1985) can be used to write fire pre-

scriptions for safely reducing this hazard. Prescribed fire can also be used to reduce the hazard associated with logging slash resulting from clearcuts and partial cuts. Most fire prescriptions can be written so as to accomplish silvicultural, range, and wildlife objectives as well as hazard reduction.

Silviculture—Where timber management is an objective, fire can be used to dispose of slash, prepare seedbeds, control species composition, and reduce the probability of stand-destroying wildfires. Ponderosa pine is often a favored timber species. It may, for example, be deemed desirable to maintain ponderosa pine dominance in stands where Douglas-fir is plagued with severe mistletoe, chronic budworm, or root rot damage. Fire can be used to remove unwanted Douglas-fir regeneration once the ponderosa pine reaches about 5 inches (about 13 cm) in diameter. Wright (1978) recommends there be an adequate number of trees 10 to 12 ft (3 to 2.7 m) tall before regular prescribed burning begins, although light surface fires will leave trees 6 to 8 ft (1.8 to 2.4 m) tall unharmed. Larger Douglas-fir trees will also survive most light surface fires, so there need be no concern about completely eliminating Douglas-fir from the stand. However, where butt rot is common on overstory Douglas-fir, increased mortality should be expected.

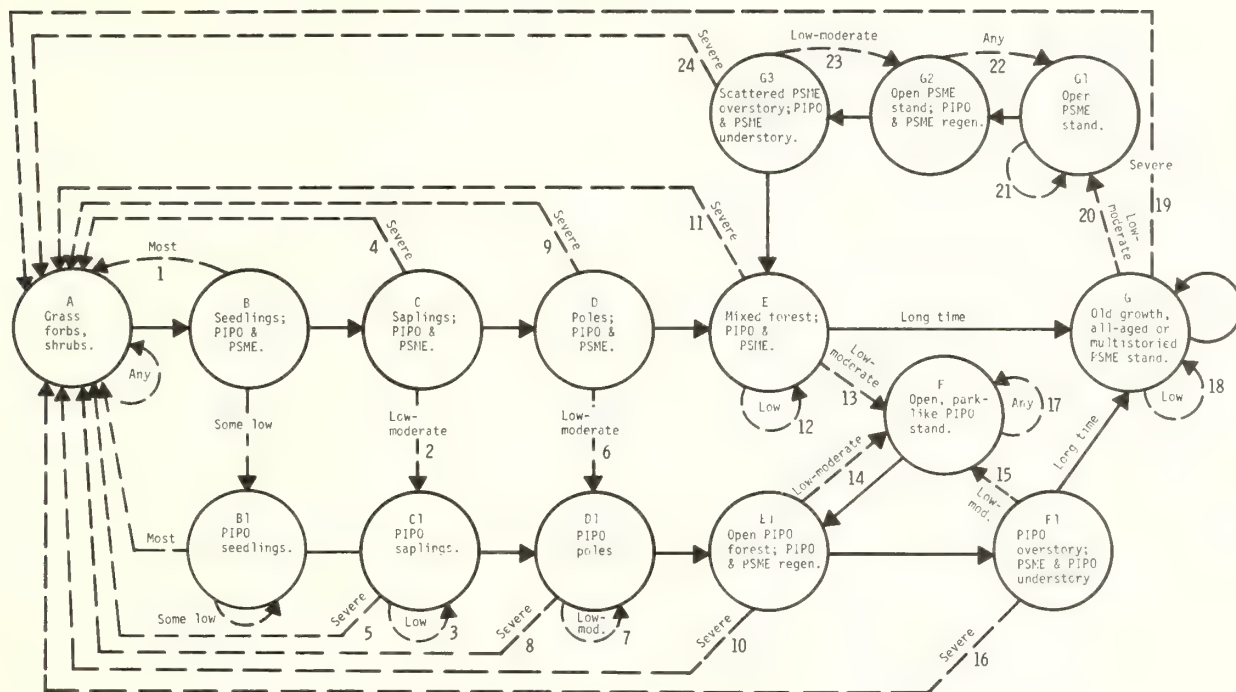
Range and Wildlife Habitat Management—Big game winter and spring range can be rejuvenated with properly applied prescribed fire, especially in the spring. Such fires can reduce encroachment by Douglas-fir, remove accumulated dead plant materials, recycle nutrients, regenerate mature and decadent shrubs, and increase distribution and production of nutrient-rich grasses, forbs, and legumes. Prescribed fires can be used to increase the nutritional value of critical wintering and fawning habitat, and thereby reduce neonatal fawn losses of mule deer (Schneeegas and Bumstead 1977). Williams and others (1980) found that deer and cattle preferred forage within a burned PSME/AGSP h.t. over unburned controls.

Recreation and Esthetics—Prescribed fire can be used to greatly reduce fire hazard on areas immediately adjoining campgrounds. Such treatment also improves viewing and travel from the campground to the surrounding forest.

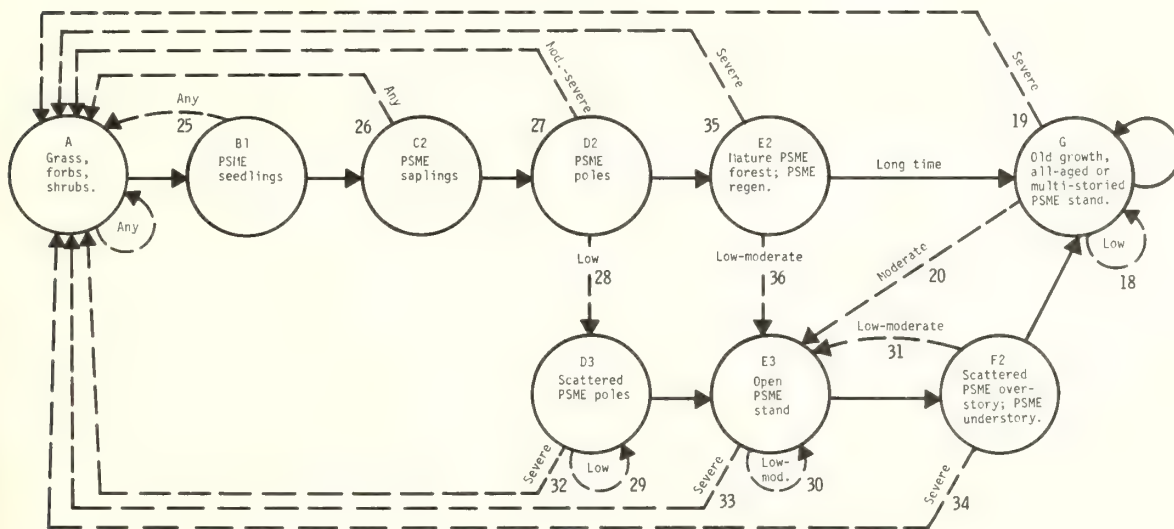
FIRE GROUP FIVE: COOL, DRY DOUGLAS-FIR HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
220	<i>Pseudotsuga menziesii</i> / <i>Festuca idahoensis</i> h.t. (PSME/FEID), Douglas-fir/Idaho fescue	Northwestern and west central
330	<i>Pseudotsuga menziesii</i> / <i>Carex geyeri</i> h.t. (PSME/CAGE), Douglas-fir/elk sedge	Northwestern and west central

1. SITES WITHIN COLD LIMITS OF PONDEROSA PINE



2. SITES ABOVE THE COLD LIMITS OF PONDEROSA PINE



LEGEND :

- Succession in absence of fire
- - -→ Response to fire
- Low Cool or light surface fire
- Mod. Fire of intermediate (moderate) severity
- Severe Hot, stand-destroying fire
- 1, 2, etc. Reference number, (see text)

Figure 9—Hypothetical fire-related successional pathways for Fire Group Four habitat types. (1) Sites within the cold limits of ponderosa pine and (2) sites above the cold limits of ponderosa pine.

Vegetation

Fire Group Five habitat types support Douglas-fir stands even under the influence of periodic fire. Douglas-fir is the indicated climax species on these sites. It dominates most seral communities and often is the only conifer present. Sites are apparently too dry for lodgepole pine and too cold for ponderosa pine. Rocky Mountain juniper, white-bark pine, and lodgepole pine may occur as accidental individuals, minor seral species, or minor climax species.

Regeneration is often difficult. On north-facing and northeast-facing slopes, however, heavily overstocked stagnant stands often develop. Undergrowth may be sparse. Common undergrowth forbs include heartleaf arnica, false Solomon's seal, mountain sweetroot, and western meadow-rue. Common grasses include bluebunch wheatgrass, elk sedge, and Idaho fescue.

Shrubs include big sagebrush, common juniper, wax currant, and white spirea.

Forest Fuels

Downed, dead fuel loads average about 10 tons per acre (about 2 kg/m²). Downed woody fuel loadings calculated by Brown and See (1981) are shown in table 6 and in figure 3.

While downed, dead woody fuel loadings are greater than in Fire Groups One, Two, Three, and Four, live fuels are less concern. Both undergrowth and regeneration are usually sparse. This factor plus the usual open nature of the stands result in a low probability of crown fire. Individual trees will often have branches close to the ground (fig. 10). If sufficient fuels are available on the ground, torching can occur.

Role of Fire

Under natural conditions, fire occurred less frequently within Group Five habitat types than it did within ponderosa pine habitat types (Groups Two and Three) or within the warmer Douglas-fir habitat types (Group Four). The relatively light fuel loads, sparse undergrowth, and generally open nature of the stands would appear to favor long fire-free intervals. However, Arno and Gruell (1983, 1986) estimate a mean fire interval of 35 to 45 years in pre-settlement stands in southwestern Montana.

Fire's role in seedbed preparation is confounded by the difficulty of regeneration to progress beyond the seedling stage on these droughty sites because of undergrowth and overstory competition. Where dense regeneration does occur, fire probably played a role as a thinning agent in sapling and pole-sized stands. Ground fire probably maintained many mature stands in an open, parklike condition. Many presettlement stands were actually maintained as seral grasslands with scattered trees inhabiting rocky microsites. The prolonged absence of fire has allowed these groves to become forest stands (Arno and Gruell 1983, 1986).

Forest Succession

The generalized forest succession discussed here and illustrated in figure 10 assumes sites are above the cold limits of ponderosa pine.

Frequent fire could maintain sites as grassland, as shown in figure 11, No. 1 (subsequent numbers in this section refer to fig. 11). A fire in the herb/shrub stage will prepare a seedbed (No. 2) for Douglas-fir seedlings. Seedling establishment is usually slow and probably requires



Figure 10—A Fire Group Five stand on a Douglas-fir/Idaho fescue h.t. This 100-year-old Douglas-fir stand has a downed dead fuel load of 6.6 tons per acre (1.5 kg/m²). Material less than 3 inches (7.6 cm) in diameter accounts for 2.8 tons per acre (0.62 kg/m²), and material more than 3 inches (7.6 cm) accounts for the remaining 3.8 tons per acre (0.85 kg/m²). Duff depth is 0.9 inch (2.3 cm).

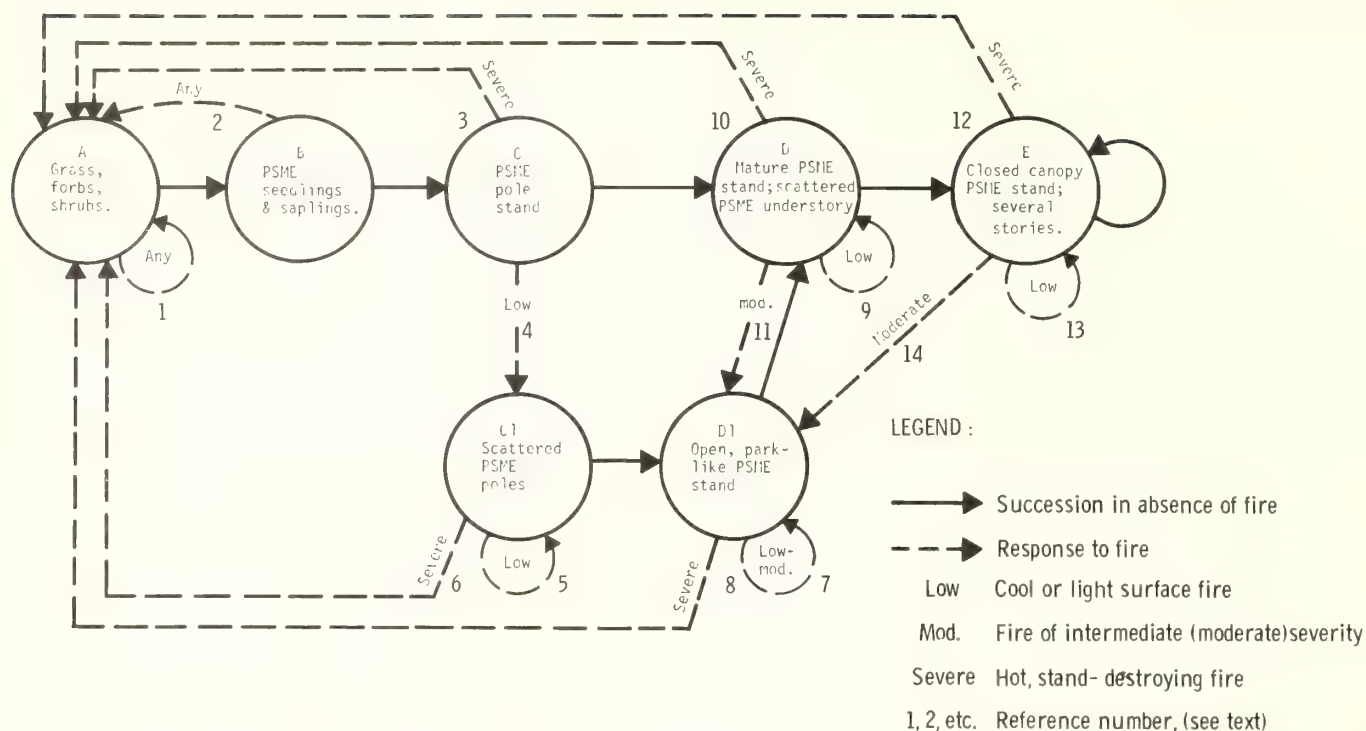


Figure 12—Hypothetical fire-related successional pathways for Fire Group Five habitat types.

FIRE GROUP SIX: MOIST DOUGLAS-FIR HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)			
250	<i>Pseudotsuga menziesii</i> / <i>Vaccinium caespitosum</i> h.t. (PSME/VACA), Douglas- fir/dwarf huckleberry	Northwestern and west central	283	<i>Pseudotsuga menziesii</i> / <i>Vaccinium globulare</i> h.t.- <i>Xerophyllum tenax</i> phase (PSME/VAGL-XETE), Douglas- fir/blue huckleberry-common beargrass phase	Northwestern and west central
261	<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> h.t.- <i>Physocarpus malvaceus</i> phase (PSME/PHMA-PHMA), Douglas-fir/ninebark-ninebark phase	Northwestern and west central	291	<i>Pseudotsuga menziesii</i> / <i>Linnaea</i> <i>borealis</i> h.t.- <i>Symphoricarpos</i> <i>albus</i> phase (PSME/LIBO- SYAL), Douglas-fir/twinflower- snowberry phase	Northwestern and west central
281	<i>Pseudotsuga menziesii</i> / <i>Vaccinium globulare</i> h.t.- <i>Vaccinium globulare</i> phase (PSME/VAGL-VAGL), Douglas- fir/blue huckleberry-blue huckleberry phase	Northwestern and west central	292	<i>Pseudotsuga menziesii</i> / <i>Linnaea</i> <i>borealis</i> h.t.- <i>Calamagrostis</i> <i>rubescens</i> phase (PSME/LIBO- CARU), Douglas-fir/twinflower- pinegrass phase	Northwestern and west central
282	<i>Pseudotsuga menziesii</i> / <i>Vaccinium globulare</i> h.t.- <i>Arctostaphylos uva-ursi</i> phase (PSME/VAGL-ARUV), Douglas-fir/blue huckleberry- kinnikinnick phase	Northwestern and west central	293	<i>Pseudotsuga menziesii</i> / <i>Linnaea</i> <i>borealis</i> h.t.- <i>Vaccinium</i> <i>globulare</i> phase (PSME/LIBO- VAGL), Douglas-fir/twinflower- blue huckleberry phase	Northwestern and west central
			312	<i>Pseudotsuga menziesii</i> / <i>Symphoricarpos albus</i> h.t.- <i>Calamagrostis rubescens</i> phase (PSME/SYAL-CARU), Douglas- fir/snowberry-pinegrass phase	Northwestern and west central
			313	<i>Pseudotsuga menziesii</i> / <i>Symphoricarpos albus</i> h.t.- <i>Symphoricarpos albus</i> phase (PSME/SYAL-SYAL), Douglas- fir/snowberry-snowberry phase	Northwestern and west central

- | | | |
|-----|---|----------------------------------|
| 322 | <i>Pseudotsuga menziesii</i> /
<i>Calamagrostis rubescens</i> h.t.-
<i>Arctostaphylos uva-ursi</i> phase
(PSME/CARU-ARUV),
Douglas-fir/pinegrass-
kinnikinnick phase | Northwestern and
west central |
| 323 | <i>Pseudotsuga menziesii</i> /
<i>Calamagrostis rubescens</i> h.t.-
<i>Calamagrostis rubescens</i> phase
(PSME/CARU-CARU),
Douglas-fir/pinegrass-pinegrass
phase | Northwestern and
west central |

Vegetation

Fire Group Six habitat types occur throughout western Montana usually at elevations of about 3,000 to 6,500 ft (about 914 to 1,981 m). Douglas-fir is both the indicated climax species and a vigorous member of seral communities. It is not uncommon for Douglas-fir to dominate all stages of succession on these sites. Ponderosa pine, western larch, and lodgepole pine are seral components whose abundance varies considerably by phase.

Whitebark pine is usually well represented at upper elevations within the PSME/CARU-CARU h.t. Subalpine fir and spruce are essentially absent. At low elevations, Group Six sites can be found on all aspects. On cooler sites, ponderosa pine becomes less important and larch and lodgepole increase in importance.

Shrubs and moist site forbs dominate the undergrowth, along with pinegrass and elk sedge. Common shrubs include mountain ninebark, common snowberry, white spirea, oceanspray, dampwoods blueberry, dwarf huckleberry, grouse whortleberry, kinnikinnick, American twinflower, and common juniper. Forbs include mountain sweetroot, warberry fairybells, common beargrass, starry false Solomon's seal, western meadowrue, heartleaf arnica, and mountain arnica.

Forest Fuels

Downed, dead fuel loads average about 12 tons per acre (less than 3 kg/m²), according to Brown and See (1981) (table 6), but can be much heavier. Inventories of photo plots (Fischer 1981a, 1981b) showed a range of from 1 to 74 tons per acre (0.2 to 16.6 kg/m²). Fuel conditions will vary according to stand density, species composition, age, and stand history. The tendency toward overstocking and the development of dense understories result in high-hazard fuel conditions in many stands. Natural thinning, snow breakage, blowdown, and insect and disease mortality operate at a high level in many stands. Relatively deep duff often develops and may contain a lot of rotten logs. Fires often smolder undetected until burning conditions become favorable for fire spread.

The most hazardous conditions occur in well-stocked stands with dense Douglas-fir understories (fig. 13). These stands are characterized by relatively large amounts of downed twigs and small stems and branchwood less than 3 inches in diameter (table 9) beneath partially fallen and standing dead saplings and small pole-sized stems.



A



B



C



D

Figure 13—Examples of high hazard fuel conditions in Fire Group Six stands in Montana. Stands 27A and 86 are Douglas-fir forests near Lincoln and Lolo, respectively. Stands 85 and 6 are lodgepole pine stands with Douglas-fir understories near Lolo. Habitat types, stand age, and fuel loadings are given in table 9.

Table 9—Fuel loadings by size class for Fire Group Six stands shown in figures 13, 14, and 15

Stand number	Habitat type-phase	Age ¹	Duff depth	Size class (inches)							Total
				0-1/4	1/4-1	1-3	3-6	6-10	10-20	20+	
				Tons/acre							
		Years	Inches								
27A	PSME/VAGL-XETE	90	1.9	0.2	0.8	1.2	1.9	5.2	1.7	0	11.0
85	PSME/VAGL-XETE	70	2.2	.5	1.9	4.3	.2	1.6	4.2	0	12.7
86	PSME/PHMA-PHMA	65	2.4	.8	1.8	3.7	.4	7.5	2.0	0	16.2
6	PSME/VAGL-XETE	80	2.1	1.2	3.1	3.1	.3	7.3	13.3	0	28.3
68	PSME/CARU-ARUV	50	1.8	.5	.7	.2	0	0	0	0	1.4
80	PSME/LIBO-VAGL	280	1.5	.3	.8	.7	.8	1.1	0	0	3.7
26A	PSME/VAGL-XETE	170	.7	.2	.4	.7	1.9	.8	0	0	4.0
14A	PSME/PHMA-PHMA	70	2.0	.9	1.8	1.2	.3	.3	0	0	4.5
78	PSME/LIBO-VAGL	320	1.9	.2	1.1	1.7	3.3	.7	31.0	0	38.0
48A	PSME/VACA	130	2.2	.2	1.0	1.2	4.2	14.9	10.2	0	31.7
95	PSME/LIBO-CARU	145	2.2	.5	1.8	5.0	10.3	25.6	9.7	0	52.9
28	PSME/VAGL-XETE	110	2.7	.3	1.5	4.3	12.2	17.0	2.0	36.6	73.9

¹Age is of overstory dominants.

The absence of dense understories results in reduced fire hazard, even in well-stocked stands (fig. 14 and table 9). However, the density of overstory trees and the presence of dead branches near ground level create a crown fire potential under severe burning conditions. Downed dead

fuel tends to accumulate over time in these stands, the result of individual tree mortality and subsequent downfall (fig. 15). Gradual accumulation of downed dead fuel greater than 3 inches in diameter (table 9) increases the damage potential of surface fires.



A



B



C



D

Figure 14—Examples of Fire Group Six stands with light fuel loadings in Montana. Stands 68 and 80 are western larch—Douglas-fir and ponderosa pine—western larch—Douglas-fir stands, respectively, near Missoula. Stand 26A is a lodgepole pine stand near Lincoln. Stand 14A is a Douglas-fir forest near Troy. Habitat types, stand age, and fuel loadings are given in table 9.



A



B



C



D

Figure 15—Examples of Fire Group Six stands with heavy fuel loadings in Montana. Stand 78 is a ponderosa pine—western larch—Douglas-fir stand near Missoula. Stand 48A is a lodgepole pine stand near Philipsburg. Stand 95 is a Douglas-fir stand near Bonita, and stand 28 is a western larch—Douglas-fir forest near Clinton. Habitat types, stand age, and fuel loadings are given in table 9.

Role of Fire

Fire history studies conducted within the PSME/CARU h.t. in southwestern Montana indicate a mean fire interval of 42 years for presettlement stands (Arno and Gruell 1983). A tentative mean fire-free interval of 15.8 years was reported by Habeck (Crane and others 1983) within a PSME/PHMA-PHMA h.t. near Missoula, MT.

Fire was an important agent in controlling density and species composition. Low to moderate severity fires converted dense stands of pole-sized or larger trees to a more open condition, and subsequent light burning maintained stands in a parklike state. Frequent low or moderate fires favored larch and ponderosa pine over Douglas-fir in stands where these species occurred. Severe fires probably occurred on dense, fuel-heavy sites and resulted in stand replacement. Stand-replacement fires favored lodgepole pine on sites where this species was present.

Fire's role as a seedbed-preparing agent is less important in this group than in those previously discussed. Douglas-fir can establish on a variety of seedbeds and is not dependent on mineral soil conditions for successful regeneration.

Fire has a demonstrable effect on wildlife habitat through its effects on food plants. The combination of opening up stands by killing overstory trees, reducing competition by removing understories, and rejuvenating sprouting plants through top kill, can significantly increase the availability of palatable browse and forage.

Fire's role as a stand replacement agent becomes more pronounced when the natural fire-free interval is increased through fire suppression, unless corresponding fuel reduction occurs.

Forest Succession

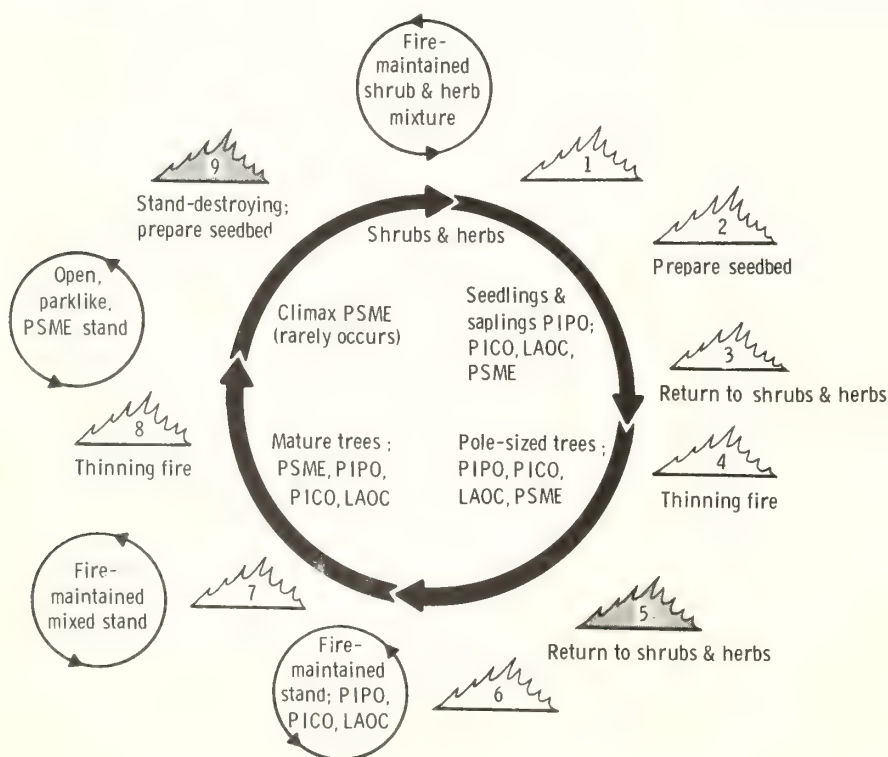
The theoretical climax condition on Group Six sites is a multistoried Douglas-fir stand, although a fire-maintained open forest condition was the normal situation during the presettlement period, as shown in figure 16 (subsequent numbers in this section refer to fig. 16). Following a severe, stand-destroying fire (No. 1), grass, forbs, and shrubs dominate the site. Subsequent fires in this stage perpetuate herbs and shrubs (No. 2). Seedlings of Douglas-fir, lodgepole pine, and larch may become established if the fire-free interval is of adequate length. A fire in the seedling stage (No. 3) most likely returns the site to herbs and shrubs, although some ponderosa pine seedlings may survive some cool fires.

Low or moderate fires in the sapling stage (No. 4) thin the stand, if ponderosa pine and western larch are dominant, or eliminate Douglas-fir and lodgepole pine where these species are major components.

Many pole-sized Douglas-fir, western larch, and ponderosa pine will survive low or moderate fires (No. 6), which may serve to increase seral species as well as thin the stand. Severe fires kill trees of all species (No. 5). If serotinous trees are present, a new stand of nearly pure lodgepole pine initiates from their seeds.

Low to moderate fires (No. 7) in mature mixed conifer stands thin them, while severe fires revert these sites to the shrub/herb stage.

Climax Douglas-fir stands are rare because of the presence of seral species whose longevity is greater than the usual fire-free interval. Climax stands are more likely to occur on sites where Douglas-fir is the seral dominant as well as the climax species, notably on sites within PSME/



LEGEND :

- ➔ GENERALIZED FOREST SUCCESSION
- 🔥 COOL FIRE
- 🔥 SEVERE FIRE

Figure 16—Generalized forest succession in Fire Group Six: moist, Douglas-fir habitat types.

PHMA-PHMA and PSME/CARU-CARU habitat types. Frequent low to moderate fires in the climax conditions on these sites will create a more open, parklike stand of Douglas-fir (No. 8), whereas a severe fire returns the stand to the shrub/herb stage (No. 9).

Group Six sites support stands whose seral development falls within one of three basic patterns: (1) where ponderosa pine and western larch are seral dominants, (2) where Douglas-fir is the only important conifer present throughout succession, and (3) where lodgepole pine and Douglas-fir together dominate the successional process. Hypothe-

sized successional pathways for stands where ponderosa pine and western larch share dominance with Douglas-fir are similar to those illustrated in figure 9 (Fire Group Four). Ponderosa pine and larch respond similarly to fire, although ponderosa pine exhibits a greater fire resistance through the small-pole stage, and larch survives moderate to severe fires better at larger diameter classes. Hypothetical successional pathways for Douglas-fir stands and mixed stands of lodgepole pine and Douglas-fir are illustrated in figure 17.

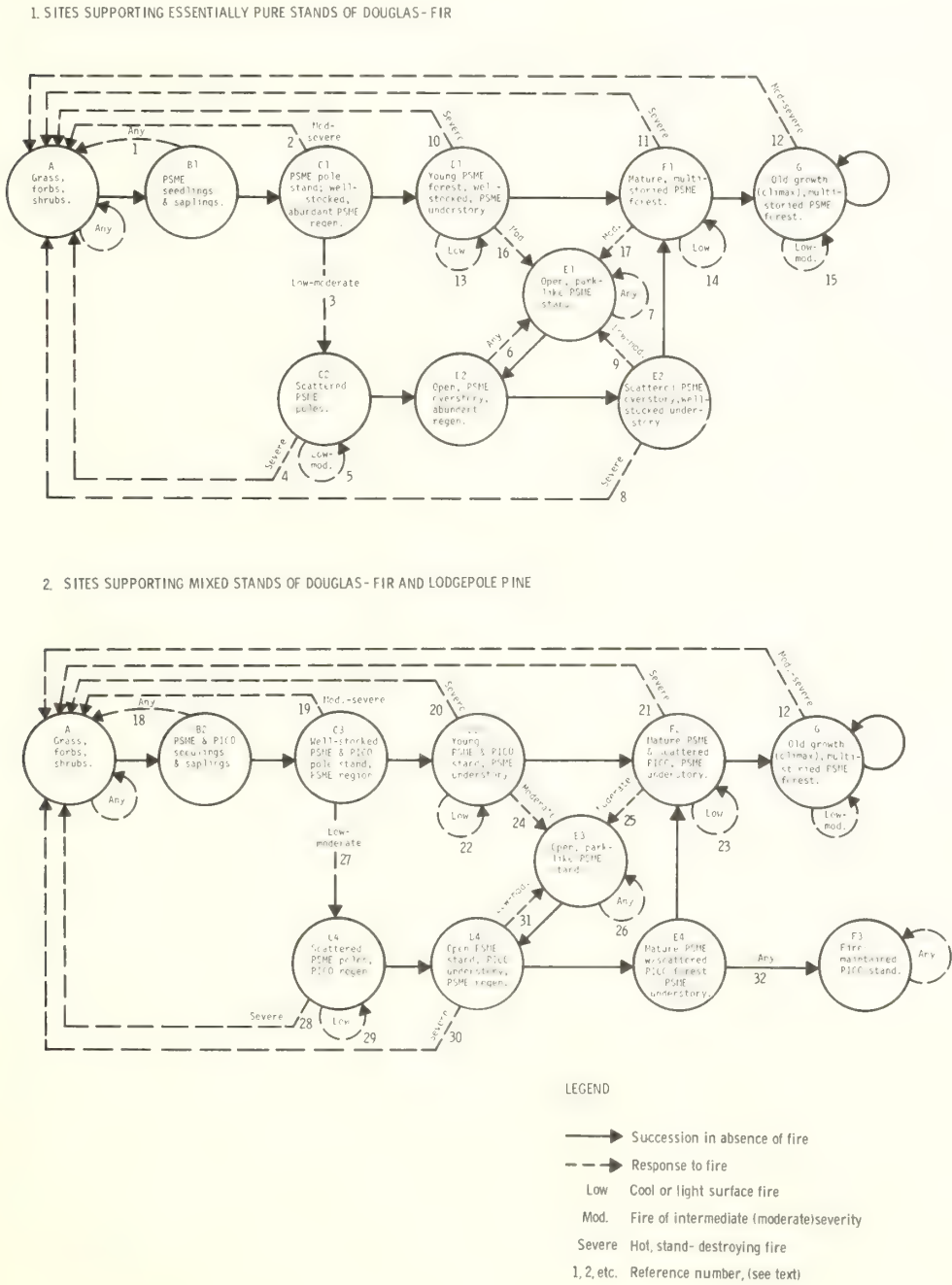


Figure 17—Hypothetical fire-related successional pathways for Fire Group Six habitat types. (1) Sites supporting essentially pure stands of Douglas-fir, and (2) sites supporting mixed stands of Douglas-fir and lodgepole pine.

The successional sequences of community types provided by Arno and others (1985) can be used as an aid in predicting successional development of seral communities within the PSME/PHMA and PSME/VAGL-XETE h.t. in relation to fire and harvest treatments.

Fire Management Considerations

Opportunities for using prescribed fire to accomplish management objectives are probably greater on Group Six sites than in any other. Often, a single fire can accomplish a variety of management objectives.

Wildfire Hazard Reduction—On sites where ponderosa pine and western larch are dominant seral components and where overstory Douglas-fir trees are large, fire can be used to reduce the risk of damage from wildfire by reducing the accumulated woody debris on the forest floor or the slash resulting from logging activities. Similarly, crown fire potential can be reduced by using fire to remove dense understories or patches of shrub and tree regeneration. Guidelines provided by Brown and others (1985) should be used to write fire prescriptions for safely reducing wildfire hazard in these stands.

Fire can be used to reduce hazard in thinning slash if ponderosa pine and western larch leave trees are 5 inches (13 cm) in diameter or larger and lower branches are high enough above the forest floor so fire will not be carried to the crown. In heavily thinned stands, slash may have to be burned when it is green to minimize damage to residual stand.

Where shaded fuelbreaks have been created, periodic prescribed fire can be used to maintain these areas in a fuel-free condition.

Silviculture—Fire can be used to favor ponderosa pine and western larch at the expense of Douglas-fir where this is silviculturally desirable. A relatively light surface fire can be used to remove Douglas-fir understories, thereby reducing the competition for moisture and nutrients. Where such fires burn hot enough to create openings in the stand, or to bare mineral soil in existing openings, ponderosa pine and western larch regeneration may become established.

On logged areas, fire can prepare sites that are immediately favorable for establishment of ponderosa pine and western larch regeneration by providing a mineral soil seedbed. Prescribed fire guidelines (Brown and others 1985) provide a basis for writing fire prescriptions that allow the manager to remove only as much duff as is necessary to obtain desired stocking. Such fires should also reduce grass and shrub competition for the new seedlings. Where large amounts of pinegrass and elk sedge are present in the understory, care should be taken to prescribe a fire hot enough to kill the root crowns. A light fire will often encourage the pinegrass and elk sedge to the detriment of tree seedlings.

Range and Wildlife Habitat Management—Fire can be used to stimulate the production of wildlife food on some sites. Light- and medium-intensity surface fires will result in increased density and nutrient content of dampwoods blueberry (blue huckleberry) and other sprouting shrubs where present. This in turn should result in increased berry production for grouse, bear, and other wildlife, as well as for humans. Highly palatable new shoot growth on dampwoods blueberry (blue huckleberry) and other sprouting shrubs will provide increased browse for deer, elk, and other wildlife. Grass and forb production may also be increased and their nutrient content temporarily enhanced. Hot surface fires will favor reproduction of conifers and shrubs such as snowbrush and ceanothus.

Fires in logging slash will often result in a tremendous increase in the abundance of palatable shrub species as well as grasses and forbs that were present in the preburn stand along with conifer seedlings. A similar situation will usually follow stand replacement wildfires.

Fire Use Considerations—When planning fire use, fire managers should use the results and recommendations reported by DeByle (1981), Miller (1977), Stark (1977), Stark and Steele (1977), Norum (1977), Beaufait and others (1977), and Steele and Beaufait (1969). Research results suggest that high-intensity fires be avoided on steep, dry south slopes.

FIRE GROUP SEVEN: COOL HABITAT TYPES USUALLY DOMINATED BY LODGEPOLE PINE

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
250	<i>Pseudotsuga menziesii</i> / <i>Vaccinium caespitosum</i> h.t. (PSME/VACA), Douglas- fir/dwarf huckleberry	Northwestern and west central
450	<i>Picea/Vaccinium caespitosum</i> h.t. (PICEA/VACA), spruce/dwarf huckleberry	Northwestern and west central
470	<i>Picea/Linnaea borealis</i> h.t. (PICEA/LIBO), spruce/ twinflflower	West central
640	<i>Abies lasiocarpa/Vaccinium</i> <i>caespitosum</i> h.t. (ABLA/VACA), subalpine fir/dwarf huckleberry	Northwestern and west central
654	<i>Abies lasiocarpa/Calamagrostis</i> <i>canadensis</i> h.t.- <i>Vaccinium</i> <i>caespitosum</i> phase (ABLA/VACA), subalpine fir/bluejoint-dwarf huckleberry phase	Northwestern and west central
663	<i>Abies lasiocarpa/Linnaea</i> <i>borealis</i> h.t.- <i>Vaccinium</i> <i>scoparium</i> phase (ABLA/ LIBO-VASC), subalpine fir/ twinflflower-grouse whortleberry phase	Northwestern and west central
692	<i>Abies lasiocarpa/Xerophyllum</i> <i>tenax</i> h.t.- <i>Vaccinium scoparium</i> phase (ABLA/XETE-VASC), subalpine fir/beargrass-grouse whortleberry phase	Northwestern and west central
720	<i>Abies lasiocarpa/Vaccinium</i> <i>globulare</i> h.t. (ABLA/VAGL), subalpine fir/blue huckleberry	West central
732	<i>Abies lasiocarpa/Vaccinium</i> <i>scoparium</i> h.t.- <i>Vaccinium</i> <i>scoparium</i> phase (ABLA/VASC-VASC), subalpine fir/grouse whortle- berry-grouse whortleberry phase	Northwestern and west central

920	<i>Pinus contorta/Vaccinium</i> <i>caespitosum</i> h.t. (PICO/VACA), lodgepole pine/dwarf huckleberry	West central
930	<i>Pinus contorta/Linnaea</i> <i>borealis</i> c.t. (PICO/LIBO), lodgepole pine/twinflower	Northwestern and west central
940	<i>Pinus contorta/Vaccinium</i> <i>scoparium</i> c.t. (PICO/VASC), lodgepole pine/grouse whortleberry	Northwestern and west central

Vegetation

Fire Group Seven contains two groups of habitat types. The first group consists of lodgepole pine climax series habitat types (and community types) that support essentially pure stands of lodgepole pine, which constitutes the persistent dominant species on these sites. The other group consists of those Douglas-fir, spruce, and subalpine fir habitat types that are usually found supporting lodgepole pine-dominated stands. Wildfires evidently recycle the stands before the lodgepole pine dies out.

Subalpine fir, spruce, Douglas-fir, and whitebark pine occur in varying amounts with lodgepole pine on most sites.

Undergrowth often consists of dense mats or layers of grasses or shrubs. The most common graminoid species are pinegrass, bluejoint, and elk sedge. Common shrubs include grouse whortleberry, dampwoods blueberry (blue huckleberry), dwarf huckleberry, American twinflower, kinnikinnick, white spirea, bunchberry dogwood, common snowberry, and creeping Oregon grape. Heartleaf arnica, broadleaf arnica, and western meadowrue are among the more common forbs.

Forest Fuels

The average downed woody loading is about 18 tons per acre (about 4 kg/m²) (table 6). Inventories of photo plots (Fischer 1981b) showed a range of about 3 to 35 tons per acre (about 0.7 to 7.8 kg/m²) (fig. 18 and table 10), but maximum loads may greatly exceed this range. Mathews (1980) reports extreme fuel loads in excess of 150 tons per acre (34 kg/m²) in west-central Montana (fig. 19).

Fuel loads are characterized by relatively large amounts of material 3 inches (7.6 cm) or more in diameter. At least half the total weight is usually contributed by large material. As a general rule, the proportion of the total fuel load made up of material 3 inches (7.6 cm) or more in diameter increases as the total load increases.



A



B



C



D

Figure 18—A range of stand conditions and fuel loadings in Group Seven lodgepole pine stands in western Montana. Stands 1 and 81 are near Lolo. Stand 24A is near Lincoln, and stand 49A is near Hamilton. Habitat types, stand age, and fuel loadings are presented in table 10.

Table 10—Fuel loadings by size class for stands shown in figure 18

Stand number	Habitat type-phase	Age ¹	Duff depth	Size class (inches)							Total
				0-1/4	1/4-1	1-3	3-6	6-10	10-20	20 +	
		<i>Years</i>	<i>Inches</i>	<i>Tons/acre</i>							
1	ABLA/VACA	80	1.4	0.6	0.9	3.8	1.4	0.4	0	0	7.1
24A	ABLA/XETE-VASC	160	.8	.3	1.0	2.5	7.7	1.3	0	0	12.8
49A	ABLA/VACA	165	2.3	.3	1.4	8.1	11.8	1.0	0	0	22.6
81	PICEA/LIBO	50	1.6	.3	.8	2.4	2.8	6.3	22.1	0	34.7

¹Age of overstory dominants.

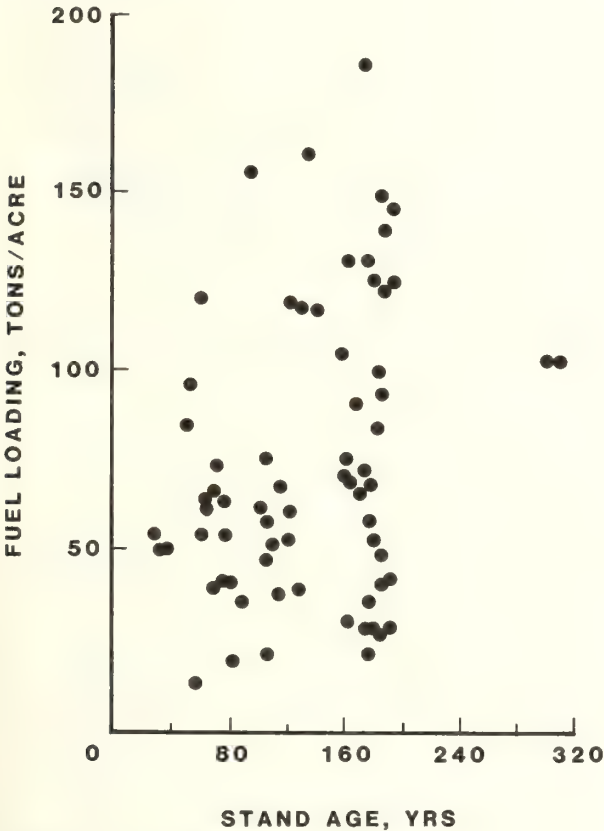


Figure 19—Fuel loading versus stand age for 71 lodgepole pine stands in the East Fork of the Bitterroot River drainage near Sula, MT (Mathews 1980).

Live fuels can be a problem but not to the extent they are in some other Fire Groups. The primary live fuel consideration is related to the occurrence of dense patches or entire stands of young lodgepole with intermingled crowns and lower branches extending down to the surface fuels. When ignited under favorable burning conditions, such stands are usually destroyed in a few minutes. Many mature stands are characterized by densely stocked, clean-boled trees with large amounts of deadfall on the forest floor (fig. 18 and table 10). An immediate source of deadfall in a young lodgepole stand is the snags

created by the previous fire. Lyon (1984) found that after 2 years with little windthrow, lodgepole pine snags on the Sleeping Child Burn (Bitterroot National Forest) fell at an annual rate of 13.4 percent (fig. 20). Overall, an average of 497 snags per acre was reduced to an average of 75 snags per acre after 15 years (table 11). After 21 years, nearly 93 percent of all snags had fallen (fig. 20).

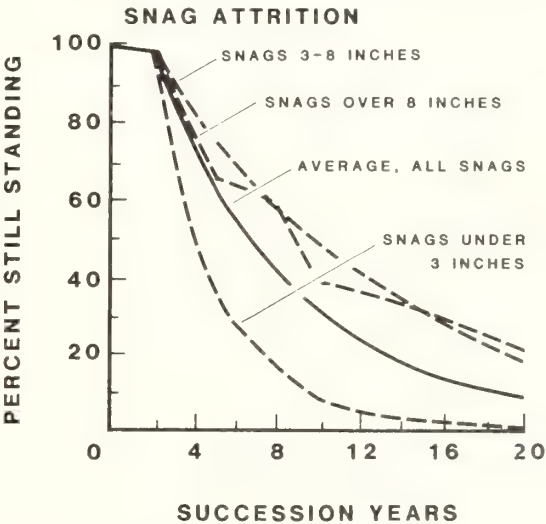


Figure 20—Percentage of lodgepole pine snags still standing, by year and diameter class, Sleeping Child Burn, Bitterroot National Forest, MT, 1962 to 1982 (Lyon 1984).

Table 11—Average number of snags per acre by size class and year of count, Sleeping Child Burn, Bitterroot National Forest, MT (Lyon 1977) (totals may not agree because of rounding)

Size class	Year					
	1962	1963	1966	1969	1971	1976
Inches						
Under 3	266	265	96	41	28	4
3 to 8	159	156	124	103	85	50
8 to 12	64	62	40	36	24	19
Over 12	7	7	7	6	4	3
Total	497	390	268	186	141	75

Aside from fire-created snags, sources of deadfall are thinning, snow breakage and windthrow of live trees, dwarf mistletoe mortality, and mountain pine beetle attack and subsequent mortality. Mountain pine beetle attack is often the mechanism that causes the lodgepole stand to break up. Cumulative mortality during a mountain pine beetle epidemic (duration of about 11 years) frequently amounts to 85 percent or more of the large, 8-inch (20-cm) diameter trees in a lodgepole pine stand (Cole and Amman 1980).

Brown (1975) has characterized fuel cycles and fire hazard in lodgepole pine stands, as shown in figure 21. Curve A of that figure corresponds to what Muraro (1971) describes as typical fire hazard in lodgepole pine where young stands, especially dense ones, are most hazardous. Least hazardous are moderately dense to open advanced, immature and mature stands. Hazard increases as stands become overmature and ground fuels build up from down-fall and establishment of shade-tolerant species. Curve C depicts conditions not uncommonly found. Ground fuel quantities and fire potential remain relatively low throughout the life of the stand until it undergoes decadence. Individual stands can vary anywhere between curves A and C during younger growth periods and develop higher fire potential at later periods of growth (curve B).

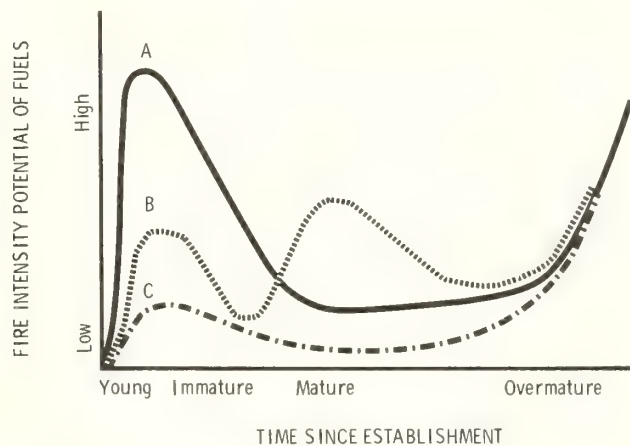


Figure 21—Fuel cycles and fire intensity potential in lodgepole pine (Brown 1975).

Role of Fire

On sites below about 7,500 ft (2,286 m) the role of fire in seral lodgepole forests is almost exclusively as an agent that perpetuates or renews lodgepole pine. Without periodic disturbance, the shade-tolerant species replace lodgepole because it does not regenerate well on duff or under shaded conditions. Fire interrupts the course of succession and increases the proportion of lodgepole with each burn. Within 50 to 100 years following a severe fire in a lodgepole-dominated stand, a reestablished lodgepole pine forest will exist even though shrubs and herbaceous cover may become dominant immediately following the burn.

Large-scale stand-replacing fires play a major role in the ecology of lodgepole pine stands. The natural periodicity of severe fires in seral lodgepole stands probably ranges from

less than 100 years to about 500 years (Hendrickson 1970). Recurring cool fires may thin the stand or otherwise rejuvenate it without doing serious damage. However, in stands greater than 60 to 80 years old, fuels build up to a hazardous level due to natural thinning, mountain pine beetle outbreaks, dwarf mistletoe infestations, and fire-killed timber (snags) from previous fires. Eventually a chance ignition sets off a major conflagration. Such a fire may cover thousands of acres. Vast tracts of lodgepole can develop in this way as the serotinous cones open and shower the burn with seeds. The Sleeping Child Burn on the Bitterroot National Forest in western Montana is an extreme example in modern times (Lyon 1984).

The almost exclusive dominance of lodgepole pine within the lodgepole pine community types is attributed in large part to fire. Pfister and others (1977) suggest the following reasons for the absence of other species on lodgepole pine climax series sites:

1. Historic, repeated wildfires over large areas may eliminate seed sources of potential shade-tolerant competitors.
2. Light ground fires may remove invading shade-tolerant competitors from the understory.
3. Dense stands may prevent regeneration of all conifers for up to 200 years in the absence of disturbance or stand deterioration.
4. Sites may be unfavorable for the establishment of other conifers. (In Montana, the best example of this situation is within the PICO/PUTR h.t.)

Above 7,500 ft (2,286 m) the role of fire in lodgepole forests appears to differ from the classic pattern. At these altitudes the fire season is relatively short, productivity is low, and mountain pine beetle activity is inhibited by low temperatures and the short growing season. Romme (1980, 1982) has estimated a mean fire interval of 300 to 400 years for stand-destroying fires in subalpine forests of Yellowstone National Park. The spread of fire is often limited. Small, lightning-caused fires burn out patches of forest several acres in area and then die out. The result may be a mosaic of age classes, not the uniform single-aged forests prevalent on many lower elevation sites (Day 1972).

Brown's (1975) discussion of fire cycles and community dynamics in lodgepole pine forests is an important source of information on the role of fire in lodgepole pine forests (fig. 22). Brown also discusses the differential effects of fires of varying severity on lodgepole pine forests. He emphasizes the critical role of fuel and duff moisture in determining fire severity and, consequently, fire effects.

The roles of fire and mountain pine beetle are inextricable in most lodgepole pine forests. The following description of this interrelationship is from Amman's (1977) "Role of the Mountain Pine Beetle in Lodgepole Pine Ecosystems."

The role of the beetle differs in conjunction with the two basic ecological roles of lodgepole pine, where lodgepole pine is seral and where it is persistent or climax. The beetles' continued role in the seral stands will depend upon the presence of fire.

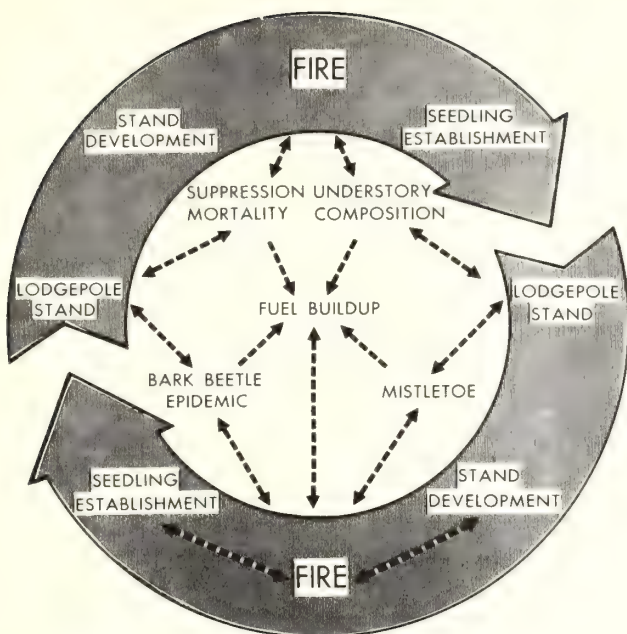


Figure 22—Lodgepole pine fire cycle showing inter-relationships among influences (Brown 1975).

Role of Mountain Pine Beetle Where Lodgepole Pine Is Seral

Absence of fire: Lodgepole pine stands depleted by the beetle and not subjected to fire are eventually succeeded by the more shade-tolerant species consisting primarily of Douglas-fir at the lower elevations and subalpine fir and Engelmann spruce at the higher elevations throughout most of the Rocky Mountains. Starting with a stand generated by fire, lodgepole pine grows at a rapid rate and occupies the dominant position in the stand. Fir and spruce seedlings also established in the stand grow more slowly than lodgepole pine.

With each infestation, the beetle kills most of the large, dominant lodgepole pines. After the infestation, both residual lodgepole pine and the shade-tolerant species increase their growth. When the lodgepole pines are of adequate size and phloem thickness, another beetle infestation occurs. This cycle is repeated at 20- to 40-year intervals depending upon growth of the trees, until lodgepole pine is eliminated from the stand.

The role played by the mountain pine beetle in stands where lodgepole pine is seral is to periodically remove the large, dominant pines. This provides growing space for subalpine fir and Douglas-fir, thus hastening succession by these species. The continued presence of the beetle in these mixed-species stands is as dependent upon fire as that of lodgepole pine. Without it, both are eliminated.

Presence of fire: Where lodgepole pine is seral, forests are perpetuated through the effects of periodic fires (Tackle 1965). Fires tend to eliminate competitive tree species such as Douglas-fir,

the true firs, and spruces. Following fire, lodgepole pine usually seeds in abundantly. Serotinous cones attached to the limbs of the tree open because of the intense heat of the fire and release their seed (Clements 1910; Lotan 1975).

Large accumulations of dead material caused by periodic beetle infestations result in very hot fires when they do occur (Brown 1975). Hot fires of this nature eliminate Douglas-fir, which otherwise is more resistant to fire damage than lodgepole pine. The dominant shade-tolerant species are eliminated, resulting in a return to a pure lodgepole pine forest. On the other hand, light surface fires would not be adequate to kill large, thick-barked Douglas-fir and return lodgepole pine to a dominant position in the stand.

Following regeneration of lodgepole pine after fire, the mountain pine beetle-lodgepole interactions would be similar to those described in the absence of fire. A fire may interrupt the sere at any time, reverting the stand back to pure lodgepole pine. However, once succession is complete, lodgepole pine seed will no longer be available to seed the burned areas except along edges where the spruce-fir climax joins persistent or climax lodgepole pine.

Role of Mountain Pine Beetle Where Lodgepole Pine Is Persistent or Climax

Lodgepole pine is persistent over large acreages, and because of the number of shade-tolerant individuals of other species found in such persistent stands, the successional status is unclear (Pfister and Daubenmire 1975). In any case, lodgepole pine persists long enough for a number of beetle infestations to occur. In such cases and those of a more limited nature when lodgepole pine is climax because of special climatic or soil conditions, the forest consists of trees of different sizes and ages ranging from seedlings to a few over-mature individuals. In these forests, the beetle infests and kills most of the lodgepole pines as they reach larger sizes. Openings created in the stand as a result of the larger trees being killed, are seeded by lodgepole pine. The cycle is then repeated as other lodgepole pines reach sizes and phloem thicknesses conducive to increases in beetle populations.

The result is two- or three-story stands consisting of trees of different ages and sizes. A mosaic of small clumps of different ages and sizes may occur. The overall effect is likely to be more chronic infestations by the beetle because of the more constant source of food. Beetle infestations in such forests may result in death of fewer trees per hectare during each infestation than would occur in even-aged stands developed after fires and in those where lodgepole pine is seral.

Fires in persistent and climax lodgepole pine forests should not be as hot as those where large epidemics of beetles have occurred. Smaller, more continuous deposits of fuel are available on the

forest floor. The lighter beetle infestations, and thus lighter accumulations of fuel, would result in fires that would eliminate some of the trees but probably would not cause total regeneration of the stand. This would be beneficial to the beetle because a more continuous supply of food would be maintained. Where large accumulations of fuel occur after large beetle epidemics, fire would completely eliminate the beetle's food supply from vast acreages for many years while the entire stand of trees grow from seedlings to sizes conducive to beetle infestation.

The mountain pine beetle's evolutionary strategies have been successful. It has exploited a niche that no other bark beetle has been able to exploit, that of harvesting lodgepole pine trees as they reach or slightly before they reach maturity. Such trees are at their peak as food for the beetle. Harvesting at this time in the age of the stand maintains the vigor of the stand, and keeps the stand at maximum productivity. (End of Amman 1977 excerpts.)

Forest Succession

The theoretical climax forest will vary according to habitat type as shown in figure 23 (subsequent numbers in this section refer to fig. 23). Except for stands within the lodgepole pine community types and the PICO/PUTR h.t., however, the climax situation is rarely achieved. Fire almost always interrupts succession before a near-climax condition develops.

Following a stand-destroying fire, a short-lived herb/shrub stage dominates. This stage is short-lived because

the lodgepole pine seedlings quickly become established and overtop the undergrowth. However, a fire in the herb/shrub stage (No. 1) will extend its period of dominance. Recurring fire at frequent intervals could conceivably maintain the site in herbs and shrubs. A fire during the seedling/sapling stage also returns the site to herbs and shrubs (No. 2). The likelihood of a fire at this stage is not great on most sites.

The effect of a fire during the pole stage depends on fire severity. A cool fire (No. 3) thins the stand while a severe fire (No. 4) destroys it. Because pole-sized lodgepole pine usually contain serotinous cone crops, periodic fire at this stage can result in a fire-maintained lodgepole pine stand. The effect of fire in a mature lodgepole forest is essentially the same as in the pole forest. A cool fire thins the stand and a severe fire recycles the stand (Nos. 5 and 6). The probability of a severe stand-destroying fire greatly increases as a previously unburned mature stand starts to break up and an understory of climax species develops. It is usually at this stage rather than the climax stage that fire destroys the stand (No. 7).

Hypothetical successional pathways for Fire Group Seven forests are illustrated in figure 24. Starting with an herb/shrub state (state A, fig. 24) two major paths exist depending on whether the site is classified as belonging to either a lodgepole pine community type or a lodgepole pine habitat type, or whether the site is a potential Douglas-fir, spruce, or subalpine fir climax.

The successional sequences of community types provided by Arno and others (1985) can be used as an aid for predicting successional development of seral communities within the ABLA/XETE-VASC h.t. in relation to various types of fire and harvest treatments.

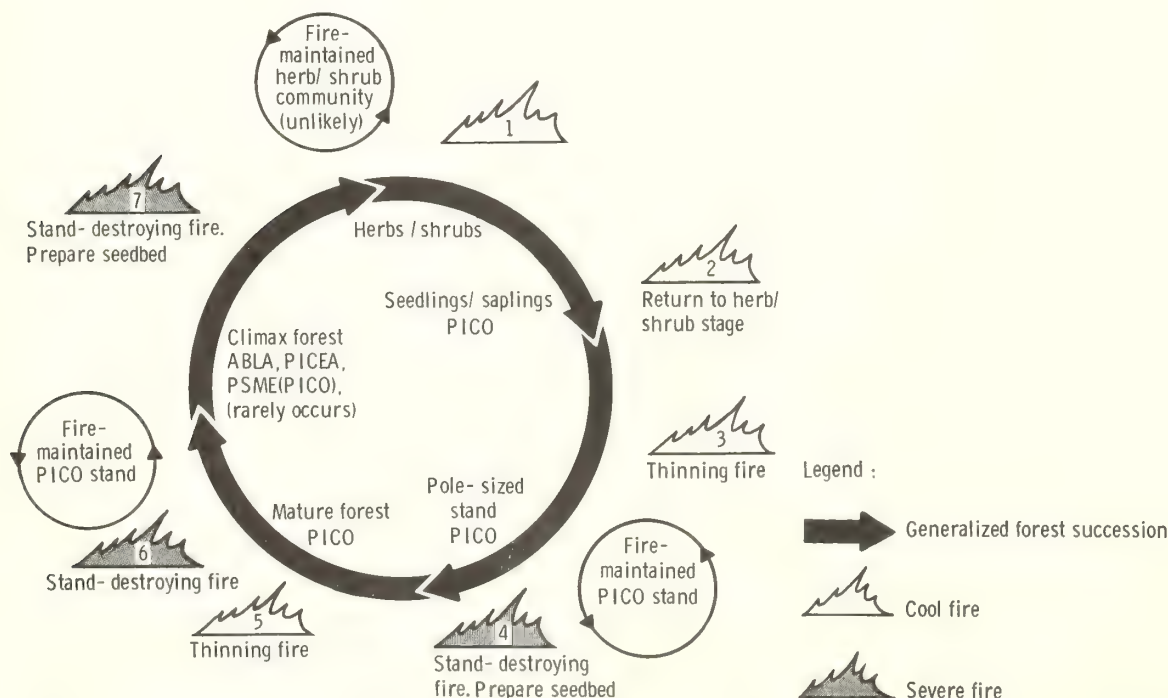
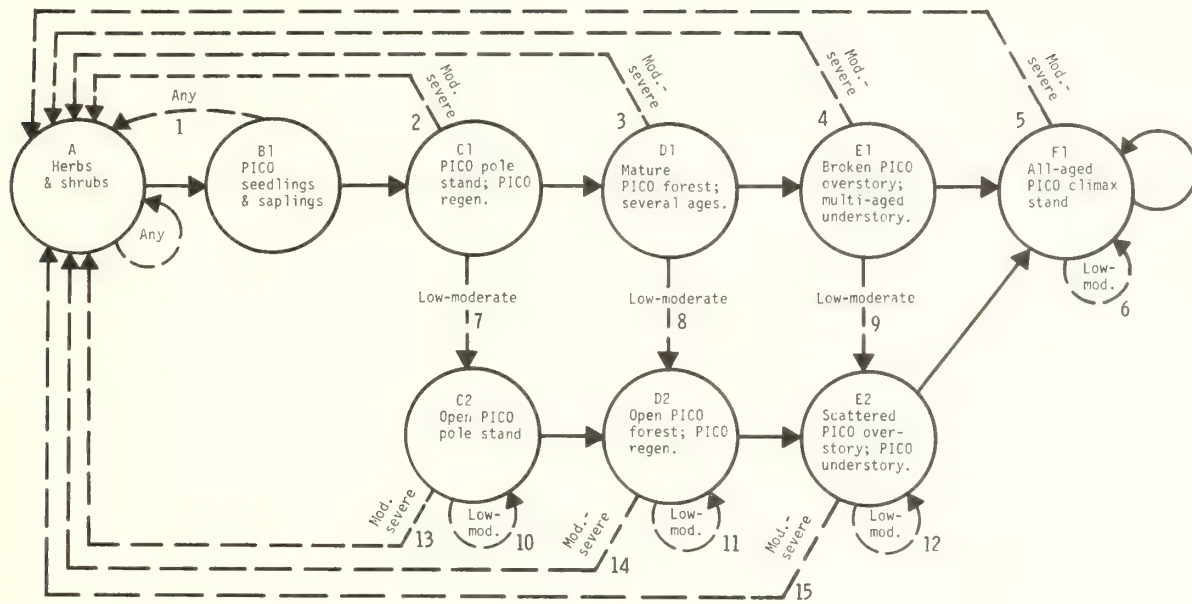


Figure 23—Generalized forest succession in Fire Group Seven: cool habitat types usually dominated by lodgepole pine.

1. LODGEPOLE PINE HABITAT TYPES



2. DOUGLAS-FIR, SPRUCE, AND SUBALPINE FIR HABITAT TYPES

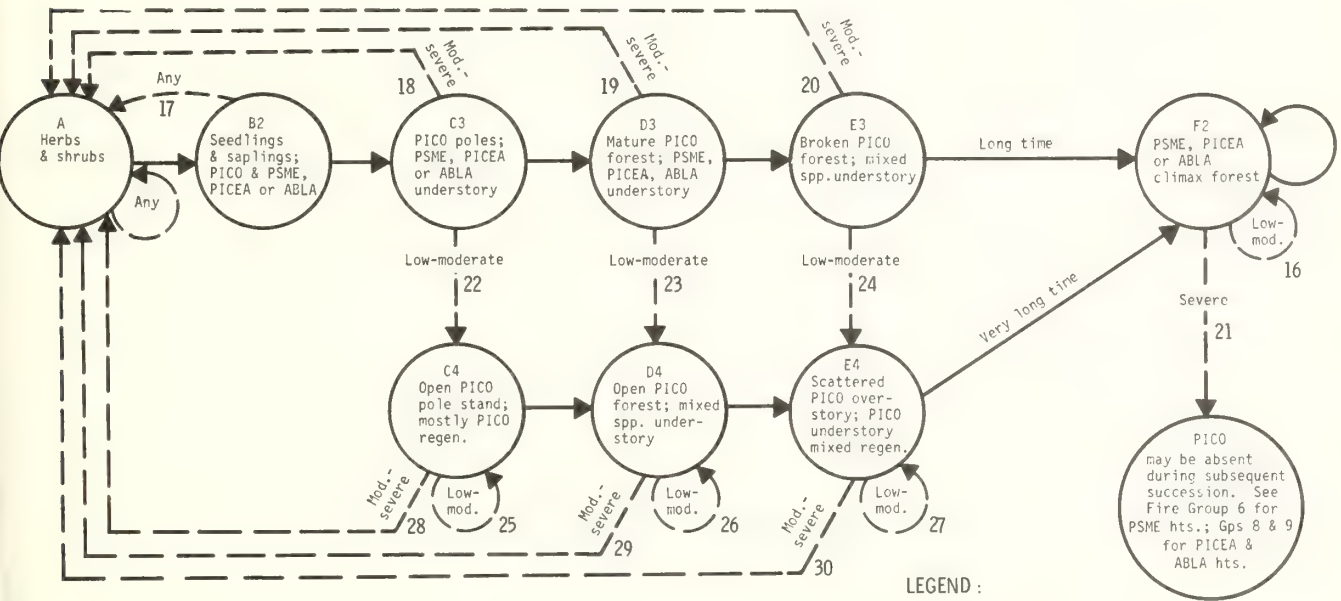


Figure 24—Hypothetical fire-related successional pathways for Fire Group Seven habitat types: (1) Lodgepole pine habitat types and (2) Douglas-fir, spruce, and subalpine fir habitat types.

Fire Management Considerations

Perhaps the primary fire management consideration in this group is protection from unwanted fire during extended periods of drought and during severe fire weather conditions. Fires at such times often crown and become holocausts if the lodgepole stand is ready physiognomically to burn (Despain and Sellers 1977).

Opportunities for fire use are limited in natural stands because of the low fire resistance of lodgepole pine, spruce, and subalpine fir. The other side of this problem is that during "safe" fire weather, it is often difficult to sustain a fire. But low- to medium-severity surface fires do occur. Thus, there may be opportunities to use prescribed fires to accomplish specific management objectives.

Prescribed fire has been suggested as a management tool for controlling dwarf mistletoe. According to Alexander and Hawksworth (1975), prescribed burning, in relation to mistletoe control, can serve two purposes: (1) eliminate infected residual trees in logged-over areas and (2) destroy heavily infected stands on unproductive sites so that they can be replaced by young healthy stands.

The primary use of prescribed fire in lodgepole pine has been and undoubtedly will continue to be for hazard reduction and site preparation in conjunction with tree harvesting and subsequent regeneration. Broadcast burning and pile and windrow burning have been the most often used methods of accomplishing these tasks. Successful broadcast slash burning usually yields increased forage production for big game. Slash disposal of any kind aids big game movement through these stands.

Lotan and Perry (1983) have summarized the various considerations that determine the appropriate use of fire for site preparation and regeneration of lodgepole pine forests (fig. 25). Silviculturists and fire managers should consult Lotan and Perry (1983) before developing fire prescriptions to regenerate lodgepole pine.

As indicated earlier, the primary concern in the fire management of many commercial lodgepole pine forests is the prevention of stand-destroying fires. Timber harvest for a variety of products, and subsequent slash disposal, are the primary means to this end. Harvest schedules should be developed and implemented to create age-class mosaics of lodgepole pine. This minimizes the areal extent of stand-destroying fires. Silvicultural practices designed to harvest trees susceptible to mountain pine beetle before the trees are attacked (Cole and Amman 1980) can greatly reduce the threat of severe fires in second-growth stands of lodgepole pine. The use of lodgepole pine for firewood, poles, posts, wood chips, and sawlogs may provide opportunities for fuel management-related harvesting.

In some wilderness areas, periodic crown fires play a

vital role in natural development of lodgepole pine ecosystems, and their use should be considered when consistent with the need to protect human life, property, and resource values outside wilderness. Fellin (1980) presents a case for fire use in lodgepole pine stands:

In many areas where natural fires have been suppressed, forest residues resulting from mountain pine beetle epidemics accumulate until hot fires occur. According to D. Cole (1978), "such fires are normally more destructive than ones that would have otherwise occurred if fires had not been suppressed, and they tend to perpetuate future extremes in the mountain pine beetle/lodgepole pine/fire interactions." Several opinions have been expressed that the bark beetle epidemics now rampant in the Rockies and Intermountain West may be a product of fire exclusion (Schwenneisen 1979). In Glacier National Park, the mountain pine beetle epidemic took such a strong hold because fire suppression programs were so successful and trees that ordinarily might have been burned are now mature and ripe for the beetles (Kuglin 1980).

D. Cole (1978) suggests that a deliberate program of fire management and prescribed fire can be instituted to moderate the mountain pine beetle-lodgepole pine-fire interaction cycle. His premise is that both wildfire and prescribed fire management plans can be developed to use fire to "create a mosaic of regenerated stands within extensive areas of timber that have developed." D. Cole (1978) believes that prescribed fires can create these ecosystem mosaics more effectively than wildfires. With the recent change from fire control to fire management, managed wildfires will be, in fact, prescribed fires.

Guidelines have been developed by McGregor and Cole (1985) to assist forest managers in integrating pest management techniques for the mountain pine beetle with other resource considerations in the process of planning and executing balanced resource management of lodgepole pine forests. The guidelines present visual and classification criteria and methods for recognizing and summarizing occurrence and susceptibility status of lodgepole pine stands according to habitat types and successional roles and important resource considerations associated with them. McGregor and Cole (1985) review appropriate silvicultural systems and practices, including use of fire, for commercial and noncommercial forest land designations including parks, wilderness, and other reserved areas.

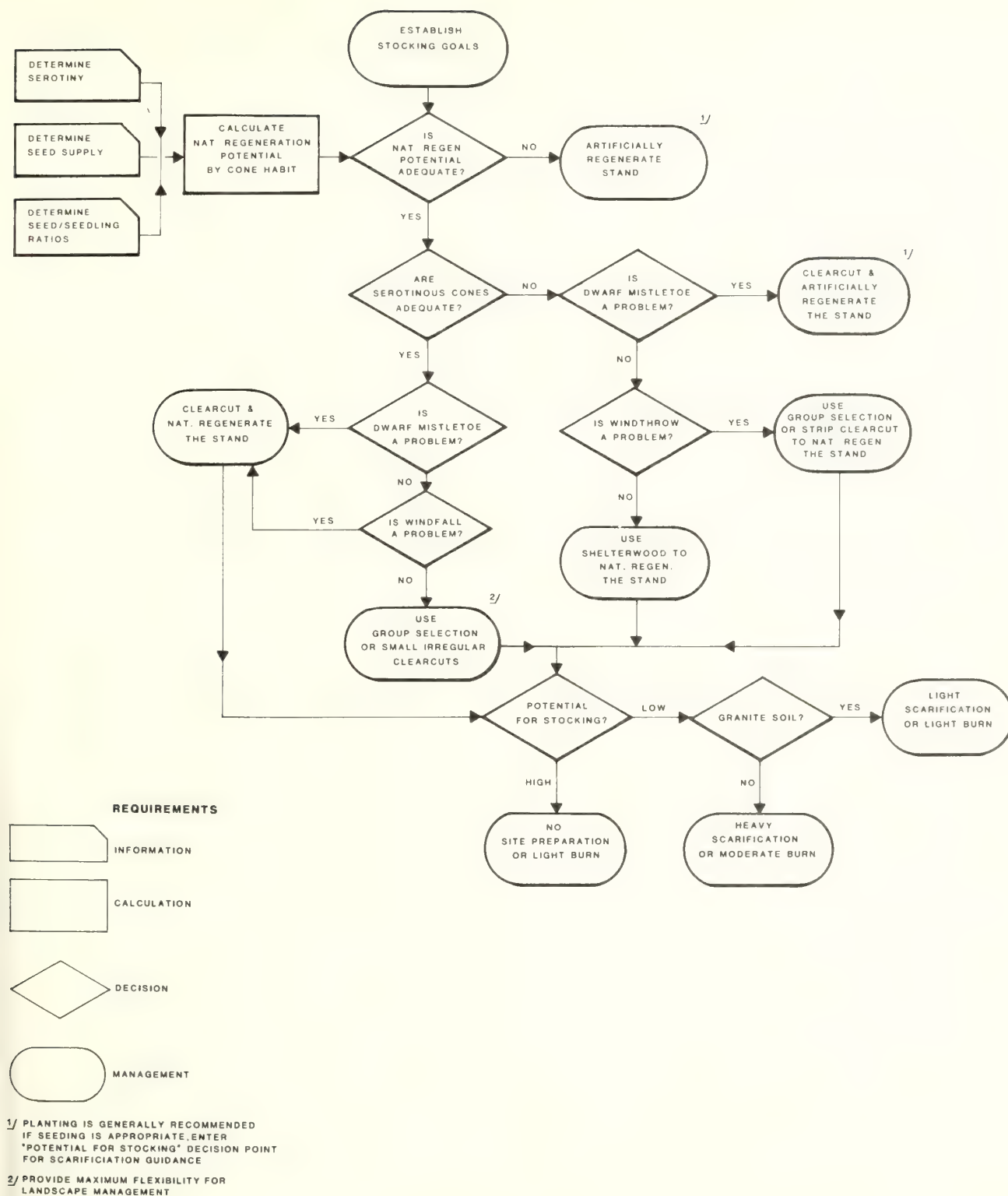


Figure 25—The decision chain for lodgepole pine regeneration (Lotan and Perry 1983).

FIRE GROUP EIGHT: DRY, LOWER SUBALPINE HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
480	<i>Picea/Smilacina stellata</i> h.t. (PICEA/SMST), spruce/starry false Solomon's seal	West central
691	<i>Abies lasiocarpa/Xerophyllum tenax</i> h.t.- <i>Vaccinium globulare</i> phase (ABLA/XETE-VAGL), subalpine fir/beargrass-blue huckleberry phase	Northwestern and west central
710	<i>Tsuga mertensiana/Xerophyllum tenax</i> h.t. (TSME/XETE), mountain hemlock/beargrass	Northwestern and west central

Vegetation

Fire Group Eight consists of dry lower subalpine habitat types where spruce, subalpine fir, or mountain hemlock are the indicated climax species. West of the Continental Divide in Montana, Fire Group Eight is represented by three habitat types: ABLA/XETE-VAGL and TSME/XETE and a minor amount of PICEA/SMST. East of the Divide, Group Eight has much greater representation (Fischer and Clayton 1983).

Douglas-fir and lodgepole pine are dominant seral species, with lesser amounts of spruce, and occasional larch or western white pine. The prevalence of Douglas-fir and lodgepole pine may be due, in part, to periodic wildfire that sets back the invasion of subalpine fir and spruce.

Stands usually contain luxuriant undergrowth. Common grasslike species are pinegrass and elk sedge. Shrub layers are dominated by one or more of the following species: mountain lover, American twinflower, common snowberry, dampwoods blueberry (blue huckleberry), and grouse whortleberry.

Among the more prevalent forbs are heartleaf arnica, broadleaf arnica, western meadowrue, pyrola, and false Solomon's seal. Solomon's seal and beargrass are also conspicuous on some sites.

Forest Fuels

Downed dead woody fuel loadings average about 18 tons per acre (about 4 kg/m²) according to Brown and See (1981) (table 6). Maximum loads may greatly exceed this value. Fuel loadings of 1 ton per acre to about 80 tons per acre (about 0.2 to 18 kg/m²) were measured during photo plot fuel inventory in western Montana (Fischer 1981b). With few exceptions, 20 tons per acre (4.5 kg/m²) represented the low end of the range of loadings encountered during photo plot inventory. The range of stand and fuel conditions is shown in figure 26.

Stands are characterized by relatively large amounts of downed woody fuel of all size classes, but especially large

amounts of material greater than 3 inches (7.6 cm) in diameter (fig. 26 and table 12).

As is the case within many subalpine fir habitat types, live fuels can contribute significantly to overall fire hazard during dry conditions. Dense understories develop in many stands and provide fuel ladders to the overstory tree crowns (fig. 27), although some stands are devoid of such understories (fig. 26).

Relatively deep duff layers may form (table 12). When the duff is dry, fire in the duff can cause considerable mortality by heating the shallow roots of subalpine fir and Engelmann spruce.

Role of Fire

Fire history data for lower subalpine habitat types in the Northern Rocky Mountains have been summarized by Arno (1980). He reported that almost 60 percent of the mature (greater than 100 years) western Montana ABLA/XETE stands sampled showed obvious evidence of ground fire after establishment.

The occurrence of periodic low- to moderate-severity fire favors Douglas-fir and lodgepole pine. Such fires set back invasion by the more tolerant subalpine fir and spruce, which in the absence of fire form dense understories and eventually take over the site. Fires of moderate severity probably help Douglas-fir maintain a position of dominance or codominance with lodgepole in many stands. The more fire-resistant Douglas-fir has a better chance of surviving such fires and is able to successfully regenerate in fire-created openings where mineral soil has been exposed. Severe, stand-destroying fire will generally favor lodgepole pine on many of these sites. Some large, thick-barked Douglas-fir trees will often survive fires severe enough to kill all the lodgepole pine trees, thereby assuring the presence of Douglas-fir in the new stand.

Before organized fire, suppression fire intervals probably fell between those reported for Fire Group Seven lodgepole pine stands (about 50 years) and those identified for the more moist lower subalpine types of Fire Group Nine (90 to 130 years).

Forest Succession

Generalized forest succession in the dry lower subalpine habitat types of Fire Group Eight is similar to the moist lower subalpine habitat types of Group Nine. The major difference between the two is that the drier Group Eight stands experience more frequent, generally less severe fires than Group Nine stands.

Because of the similarity of fire-related forest succession in the two groups, generalized forest succession is jointly discussed under Fire Group Nine. Similarly, successional pathways for Fire Group Eight are presented with those of Fire Group Nine.

The successional sequences of community types provided by Arno and others (1985) can be used as an aid in predicting successional development of seral communities within the ABLA/XETE-VAGL h.t. in relation to fire and harvest treatments.



A



B



C



D



E



F



G



H

Figure 26—Examples of Fire Group Eight stand and fuel conditions in western Montana. All of these ABLA/XETE-VAGL h.t.'s support Engelmann spruce-subalpine fir stands except stands 61 and 42, which are lodgepole pine and interior Douglas-fir respectively. Stand age and fuel loadings are given in table 12.

Table 12—Fuel loadings by size class for stands shown in figures 26 and 27

Stand number	Habitat type-phase	Age ¹	Duff depth	Size class (inches)							Total
				0-1/4	1/4-1	1-3	3-6	6-10	10-20	20+	
		Years	Inches	Tons/acre							
45	ABLA/XETE-VAGL	90	1.3	0.3	0.6	0.3	0.1	0	0	0	1.3
2A	ABLA/XETE-VAGL	80	2.2	.6	1.5	2.9	2.3	2.0	0	0	9.3
61	ABLA/XETE-VAGL	140	2.8	.5	1.7	1.3	5.2	11.5	4.1	0	24.8
42	ABLA/XETE-VAGL	335	1.1	.4	1.9	2.5	1.6	2.9	5.4	11.9	26.6
23A	ABLA/XETE-VAGL	150	3.1	.6	1.9	3.2	11.7	16.3	0	0	33.7
59	ABLA/XETE-VAGL	120	1.3	.4	1.4	2.1	9.4	24.7	2.8	0	40.8
51	ABLA/XETE-VAGL	210	3.2	.5	2.7	4.1	5.8	18.6	14.7	2.9	49.3
20A	ABLA/XETE-VAGL	165	3.4	.5	1.4	3.8	16.7	22.0	6.6	0	51.0
38	ABLA/XETE-VAGL	200	2.9	.2	1.4	5.0	11.8	47.1	11.8	0	77.3

¹Age of overstory dominants.



Figure 27—An example of a Fire Group Eight Engelmann spruce-subalpine fir stand with a high crowning potential caused by a dense understory. Stand age and fuel loadings are given in table 12.

Fire Management Considerations

Fire protection is usually an important fire management consideration during severe burning conditions especially where timber production is a management objective. When conditions are less than severe, fires may be of low to moderate severity and result in only moderate damage or no damage to overstory trees, despite the relatively low resistance of many of the species present.

Fire can be used to dispose of logging slash on harvest areas, but broadcast burning for site preparation is often hampered by high duff moisture and scarcity of acceptable burning days during traditional fall prescribed burning periods.

Where timber production is not a management objective, opportunities may exist for the use of prescribed fires to accomplish fire management (Fischer 1984). Such fires can create vegetative mosaics that in turn provide a diversity of wildlife habitats, diverse scenery, and enhanced recreational opportunities. Vegetative mosaics can also reduce the probability of widespread wildfire damage to watershed values.

FIRE GROUP NINE: MOIST, LOWER SUBALPINE HABITAT TYPES

ADP code	Habitat type-phase	Montana forest region
	(Pfister and others 1977)	(Arno 1979)
410	<i>Picea/Equisetum arvense</i> h.t. (PICEA/EQAR), spruce/common horsetail	Northwestern
420	<i>Picea/Clintonia uniflora</i> h.t.- <i>Vaccinium caespitosum</i> phase (PICEA/CLUN-VACA), spruce/queencup beadlily-dwarf huckleberry phase	Northwestern
422	<i>Picea/Clintonia uniflora</i> h.t.- <i>Clintonia uniflora</i> phase (PICEA/CLUN-CLUN), spruce/queencup beadlily-queencup beadlily phase	Northwestern
440	<i>Picea/Galium triflorum</i> h.t. (PICEA/GATR), spruce/sweetscented bedstraw	West central
610	<i>Abies lasiocarpa/Oplopanax horridum</i> h.t. (ABLA/OPHO), subalpine fir/devil's club	Northwestern
621	<i>Abies lasiocarpa/Clintonia uniflora</i> h.t.- <i>Clintonia uniflora</i> phase (ABLA/CLUN-CLUN), subalpine fir/queencup beadlily-queencup beadlily phase	Northwestern and west central
622	<i>Abies lasiocarpa/Clintonia uniflora</i> h.t.- <i>Aralia nudicaulis</i> phase (ABLA/CLUN-ARNU), subalpine fir/queencup beadlily-wild sarsaparilla phase	Northwestern and west central

623	<i>Abies lasiocarpa/Clintonia uniflora</i> h.t.- <i>Vaccinium caespitosum</i> phase (ABLA/CLUN-VACA), subalpine fir/queencup beadlily-dwarf huckleberry phase	Northwestern and west central
624	<i>Abies lasiocarpa/Clintonia uniflora</i> h.t.- <i>Xerophyllum tenax</i> phase (ABLA/CLUN-XETE), subalpine fir/queencup beadlily-beargrass phase	Northwestern and west central
625	<i>Abies lasiocarpa/Clintonia uniflora</i> h.t.- <i>Menziesia ferruginea</i> phase (ABLA/CLUN-MEFE), subalpine fir/queencup beadlily-menziesia phase	Northwestern and west central
630	<i>Abies lasiocarpa/Galium triflorum</i> h.t. (ABLA/GATR), subalpine fir/sweetscented bedstraw	West central
651	<i>Abies lasiocarpa/Calamagrostis canadensis</i> h.t.- <i>Calamagrostis canadensis</i> phase (ABLA/CACA-CACA), subalpine fir/bluejoint-bluejoint phase	West central
653	<i>Abies lasiocarpa/Calamagrostis canadensis</i> h.t.- <i>Galium triflorum</i> phase (ABLA/CACA-GATR), subalpine fir/bluejoint-sweetscented bedstraw phase	West central
661	<i>Abies lasiocarpa/Linnaea borealis</i> h.t.- <i>Linnaea borealis</i> phase (ABLA/LIBO-LIBO), subalpine fir/twinflower-twinflower phase	Northwestern and west central
662	<i>Abies lasiocarpa/Linnaea borealis</i> h.t.- <i>Xerophyllum tenax</i> phase (ABLA/LIBO-XETE), subalpine fir/American twinflower-common beargrass phase	Northwestern and west central
670	<i>Abies lasiocarpa/Menziesia ferruginea</i> h.t. (ABLA/MEFE), subalpine fir/menziesia	Northwestern and west central
680	<i>Tsuga mertensiana/Menziesia ferruginea</i> h.t. (TSME/MEFE), mountain hemlock/menziesia	Northwestern and west central
740	<i>Abies lasiocarpa/Alnus sinuata</i> (ABLA/ALSI), subalpine fir/Sitka alder	West central

Vegetation

Fire Group Nine is a collection of moist and wet lower subalpine habitat types in the spruce and subalpine fir climax series. Soils are moist or wet (supersaturated with water) much of the year. Elevations range from about 2,900 to 7,500 ft (892 to 2,308 m).

Engelmann spruce is usually a major component of seral stands along with lodgepole pine and Douglas-fir. Older stands are usually dominated by subalpine fir and spruce although Douglas-fir and lodgepole may be well represented in the overstory. Notable exceptions to this general pattern of species composition occur within the ABLA/CACA h.t., which is too wet for Douglas-fir, and within the PICEA/EQAR h.t., where spruce is usually the only successful conifer. However, two broadleaf species, paper birch and black cottonwood, may be abundant in seral stands within the PICEA/EQAR h.t. Whitebark pine occurs either accidentally or on some sites as a minor seral component.

Abundant undergrowth occurs on these moist sites. The more common grass and forb species include red baneberry, wild sarsaparilla, broadleaf arnica, bluejoint, pinegrass, queencup beadlily, field horsetail, sweetscented bedstraw, Richardson's geranium, sidebells shineleaf, arrowleaf groundsel, twisted stalk, darkwoods violet, common beargrass, and many other wet-site forbs.

Among the shrubs that occur within more than one habitat type or phase are Sitka alder, redosier dogwood, twinflower, Utah honeysuckle, rusty menziesia, thimbleberry, dampwoods blueberry (blue huckleberry), dwarf

huckleberry, and grouse whortleberry. Less widespread but abundant on particular habitats are kinnikinnick, bunchberry dogwood, western wintergreen, manyleaf swampl laurel, prickly currant, russet buffaloberry, common snowberry, and devil's club.

Forest Fuels

Fire Group Nine fuels are similar to those found in Fire Group Eight. Downed dead woody material on the forest floor averages about 25 tons per acre (about 5.6 kg/m²) (table 6) but may be much higher.

A large percentage of the downed woody fuel is material greater than 3 inches (6.7 cm) in diameter (figs. 28 and 29, and table 13). The combination of deep duff and large amounts of dead rotten fuel can result in severe surface fire during unusually dry moisture conditions. Where dense understories exist (fig. 30), such fires can easily spread to the tree crowns and destroy the stand. Even if a severe surface fire does not crown, there is a good chance the overstory trees will be killed by cambium heating.

Under normal moisture conditions for these sites, a lush undergrowth of shrubs and herbs usually serves as an effective barrier to rapid fire spread (fig. 31).

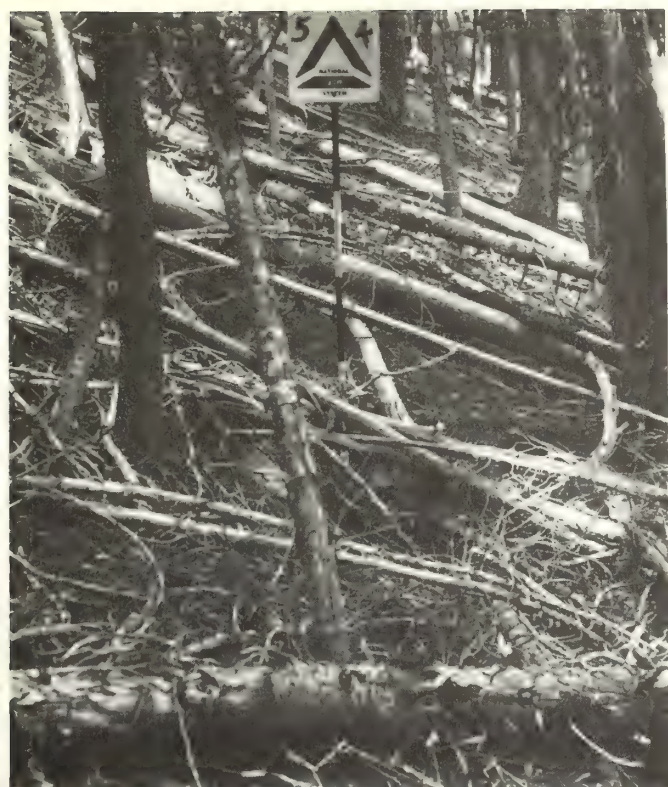


A



B

Figure 28—Examples of characteristic light to moderate fuel loadings for Fire Group Nine stands. All of these ABLA/MEFE h.t.'s support Engelmann spruce-subalpine fir stands except stand 33, which is larch—Douglas-fir. Stand age and fuel loadings are given in table 13.



C



D



E



F

Figure 28— (Con.)



A



B



C



D

Figure 29—Examples of characteristic heavy fuel loadings for Fire Group Nine stands. Stands 20 and 3 are on ABLA/CLUN-MEFE h.t.'s. Stands 93, 47, and 10 are ABLA/MEFE. And stand 62 is a ABLA/GATR. Stand age and fuel loadings are given in table 13.



E



F

Figure 29— (Con.)

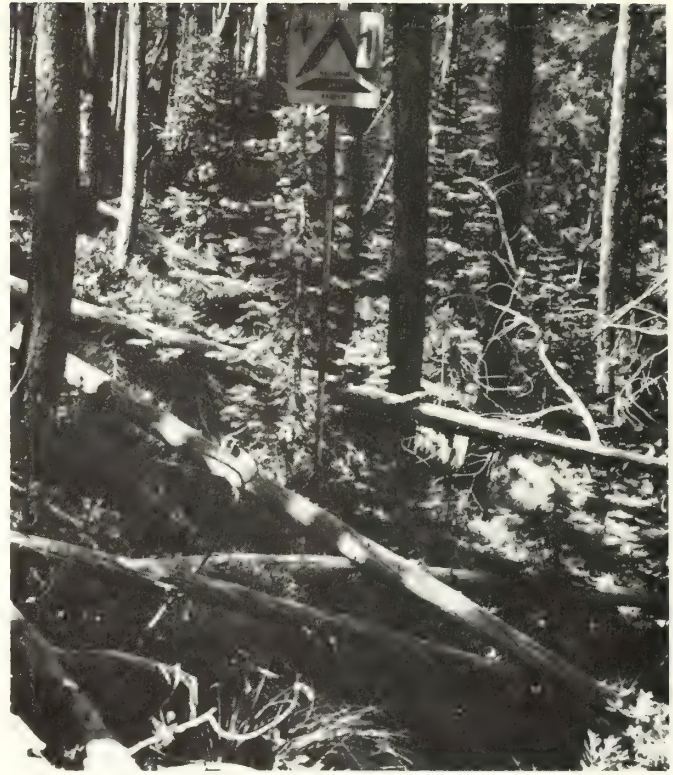
Table 13—Fuel loadings by size class for stands shown in figures 28, 29, 30, and 31

Stand number	Habitat type-phase	Age ¹	Duff depth	Size class (inches)							Total
				0-1/4	1/4-1	1-3	3-6	6-10	10-20	20+	
		Years	Inches	Tons/acre							
40	ABLA/MEFE	70	2.5	0.2	1.8	1.6	1.4	1.5	0	0	6.5
39	ABLA/MEFE	130	1.2	.1	.4	1.4	3.3	3.0	0	0	7.2
35	ABLA/MEFE	110	.9	.2	1.0	3.3	4.5	0	0	0	9.0
82	ABLA/LIBO-LIBO	55	1.5	.3	.3	1.5	1.7	7.3	1.6	0	12.7
21A	ABLA/MEFE	175	2.5	.2	.9	1.9	9.7	7.5	0	0	20.2
54	ABLA/MEFE	295	2.5	.7	2.7	4.1	6.8	6.0	1.5	0	21.8
41	ABLA/MEFE	105	1.4	.2	1.1	2.9	8.3	7.3	2.1	0	21.9
36	ABLA/MEFE	190	2.6	.4	2.0	2.9	8.1	8.9	0	0	22.3
22A	ABLA/MEFE	185	1.9	.5	1.8	2.0	5.9	9.4	2.9	0	22.5
19	ABLA/MEFE	120	1.2	.3	.9	2.9	7.7	14.6	1.6	0	28.0
57	ABLA/CLUN-MEFE	150	4.0	.2	1.1	.6	1.7	11.1	17.8	0	32.5
96	ABLA/MEFE	250	2.8	.7	1.6	1.8	4.4	17.2	7.8	0	33.5
33	ABLA/MEFE	134	2.5	.5	2.9	12.9	13.0	2.2	5.4	0	36.9
20	ABLA/CLUN-MEFE	110	3.4	.7	1.6	3.5	4.6	6.0	23.5	0	39.9
93	ABLA/MEFE	180	2.3	.7	1.5	2.3	3.8	14.3	22.7	0	45.3
47	ABLA/MEFE	350	2.6	.8	2.6	6.8	4.6	4.3	27.6	0	46.7
62	ABLA/GATR	65	4.1	.7	1.6	1.3	1.3	3.2	6.7	35.8	50.6
10	ABLA/MEFE	90	2.7	1.1	3.2	2.2	12.5	28.8	11.7	0	59.5
52	ABLA/MEFE	175	2.9	.5	2.8	2.6	4.5	16.3	32.8	3.3	62.8
3	ABLA/CLUN-MEFE	140	4.5	.4	.9	.5	2.7	7.7	57.1	3.3	72.6

¹Age is of overstory dominants.



A



B



C



D

Figure 30—Examples of high crown fire potential caused by dense under-
stories on Group Nine habitats. Stand 82 is an Engelmann spruce-subalpine fir
stand on an ABLA/LIBO h.t. Stand 41 is an ABLA/MEFE h.t. supporting a
lodgepole pine forest. Stands 36 and 52 are Engelmann spruce-subalpine fir
stands on an ABLA/MEFE h.t. Stand age and fuel loadings are given in
table 13.



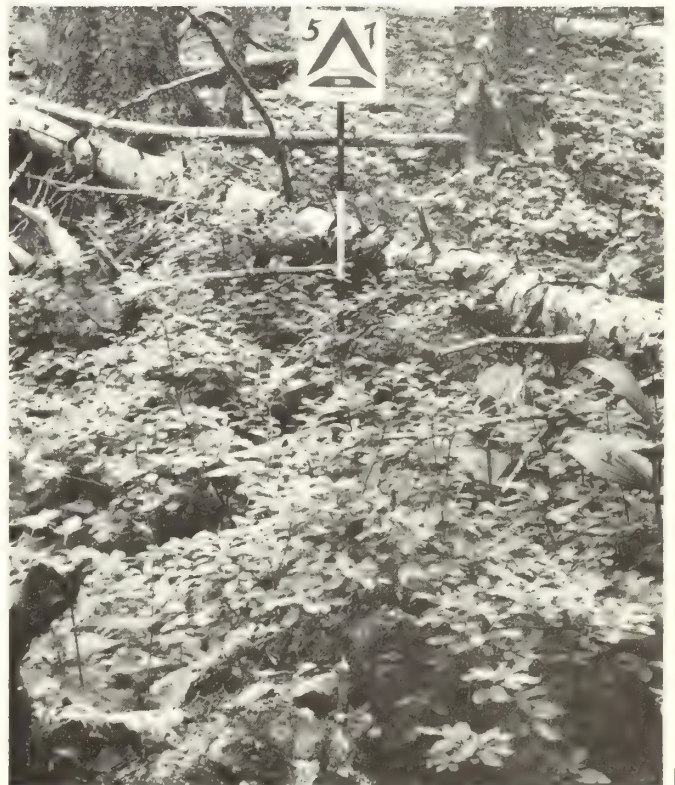
A



B



C



D

Figure 31—Examples of lush undergrowth that under normal moisture conditions retards fire spread in Fire Group Nine habitat types. Stand 57 is an Engelmann spruce-subalpine fir stand on an ABLA/CLUN-MEFE h.t. All others are ABLA/MEFE. Stand age and fuel loadings are given in table 13.

Role of Fire

Fire history information for moist, lower subalpine habitat types is limited. Mean fire-free intervals are probably longer than those of the drier upland sites in Fire Group Eight.

Sneck (1977) studied the fire history within the ABLA/CLUN h.t. at Coram Experimental Forest in northwestern Montana. She found that mean fire-free intervals ranged with topography: intervals of greater than 117 years in valleys, 121 years on mountain slopes, and 146 years on lower alpine slopes. The average of these intervals is 128 years. Fires at Coram were reported to be small, moderately severe surface fires that occasionally crowned, especially near the ridgetops. These fires thinned stands and prepared a mineral seedbed for conifer regeneration. Small, moderate-severity fires were typical at Coram, which is mesic and discontinuous of fuels. Infrequent, widespread, severe fires have been documented for the somewhat drier surrounding habitats (Sneck 1977; Arno 1980).

Freedman (1983) studied fire history within the ABLA/CLUN h.t. and PICEA/CLUN h.t. in the Goat Creek area of the upper Swan Valley near Condon, MT. Collectively, these moist forest types had adjusted fire-free intervals (Arno and Peterson 1983) of about 30 years before 1905, with extremes between 10 and 100 years (Freedman and Habeck 1985). Freedman's study sites contained abundant ponderosa pine, which may account for the rather high fire frequencies.

The impact of fire on Group Nine sites west of the Divide in Montana is indicated by stand condition and species composition. The general absence of spruce, subalpine fir, or mountain hemlock climax condition is evidence of disturbance by past fires. The dominance of lodgepole pine, Douglas-fir, larch, or spruce on many sites suggests these stands developed on a fire-created mineral soil seedbed. Frequent moderate to severe fires may be restricted in their occurrence because many mature stands have an overstory that includes fire-sensitive spruce and lodgepole.

The frequency of light surface fires is difficult to surmise. The moist nature of these sites would limit the opportunity for such fires to a brief period during the summer. It seems reasonable to assume that lightning did in fact start such fires and that a certain amount of fuel reduction was accomplished. Left undisturbed, these fires probably flared up occasionally and created openings that favored establishment of seral species.

Forest Succession

The general pattern of succession for Fire Groups Eight and Nine forests is quite similar. Both groups share many of the same seral and climax tree species, and so have much the same fire response. The two groups are primarily distinguished by the frequency and severity of fire. The following discussion of generalized fire-related forest succession applies to both groups.

In theory, the drier habitat types (Fire Group Eight) should have more frequent fires, particularly those of low to moderate severity. These fires would maintain stands in

a seral condition. Because of their moist conditions, habitat types in Fire Group Nine should have lower fire frequency. The relatively high loadings of both live and dead fuels, combined with periodic summer drought, increase the chance for severe, stand-replacing burns when fires do occur.

The potential climax forest would be composed of pure stands of subalpine fir, spruce, or mountain hemlock. The climax situation on any of these sites requires a long time to develop and, consequently, is rarely found. The near-climax condition is more common. It is often characterized by a dense understory of subalpine fir, spruce, and mountain hemlock, while Douglas-fir, lodgepole pine, and often spruce form the overstory. In northwestern Montana, larch or white pine may be the dominant overstory species.

A stand-destroying fire in the climax or near-climax stage results in an herb/shrub stage (fig. 32, No. 1), followed by a seedling/sapling stage (subsequent numbers in this section refer to fig. 32). Seedlings and saplings may be Douglas-fir, lodgepole pine, larch, white pine, or spruce. Species composition varies with site conditions. Douglas-fir or lodgepole pine frequently dominate. Whitebark pine seedlings may occur as accidentals, and some subalpine fir may be present in the initial stand.

Any fire in the seedling/sapling stage reverts the stand to the shrub/herb condition (No. 2). Moderate fires in pole-sized stands (No. 3) will favor the more fire-resistant Douglas-fir, larch, or possibly western white pine over lodgepole pine, spruce, mountain hemlock, or subalpine fir. A severe fire (No. 4) destroys the stand. Where serotinous lodgepole pine is present, seedlings of this species form a pure or nearly pure stand.

In the continued absence of fire, a mature stand develops. Lodgepole pine, Douglas-fir, larch, or white pine dominate the overstory, beneath which is a dense understory of subalpine fir, spruce, and mountain hemlock. A cool fire (No. 5) removes this understory and some of the lodgepole pine, thereby favoring the reproduction of Douglas-fir, larch, or white pine.

A moderate or severe fire could remove much of the Douglas-fir, leaving the site to be regenerated by either serotinous lodgepole pine or remnant larch. Some severe fires remove even the fire-resistant larch. In this case, or where there are severe fires in near-climax stands, the site returns to a treeless condition (No. 6). If fire does not occur for a long time, the near-climax stand may develop to the climax state, although a fire-free interval of this length is unlikely.

In each stage of stand development discussed, Fire Group Nine sites have less chance of burning than those in Group Eight because of their generally more mesic conditions.

Two potential successional pathways are hypothesized for Fire Groups Eight and Nine (fig. 33). They are distinguished primarily by their inclusion of either lodgepole pine or western larch with Douglas-fir as the major seral species. The complete separation of larch and lodgepole is somewhat artificial. It is possible for both to occur on the same site, although one species is usually more common.

Fire history information for subalpine habitat types is limited, particularly for moist Fire Group Nine sites.

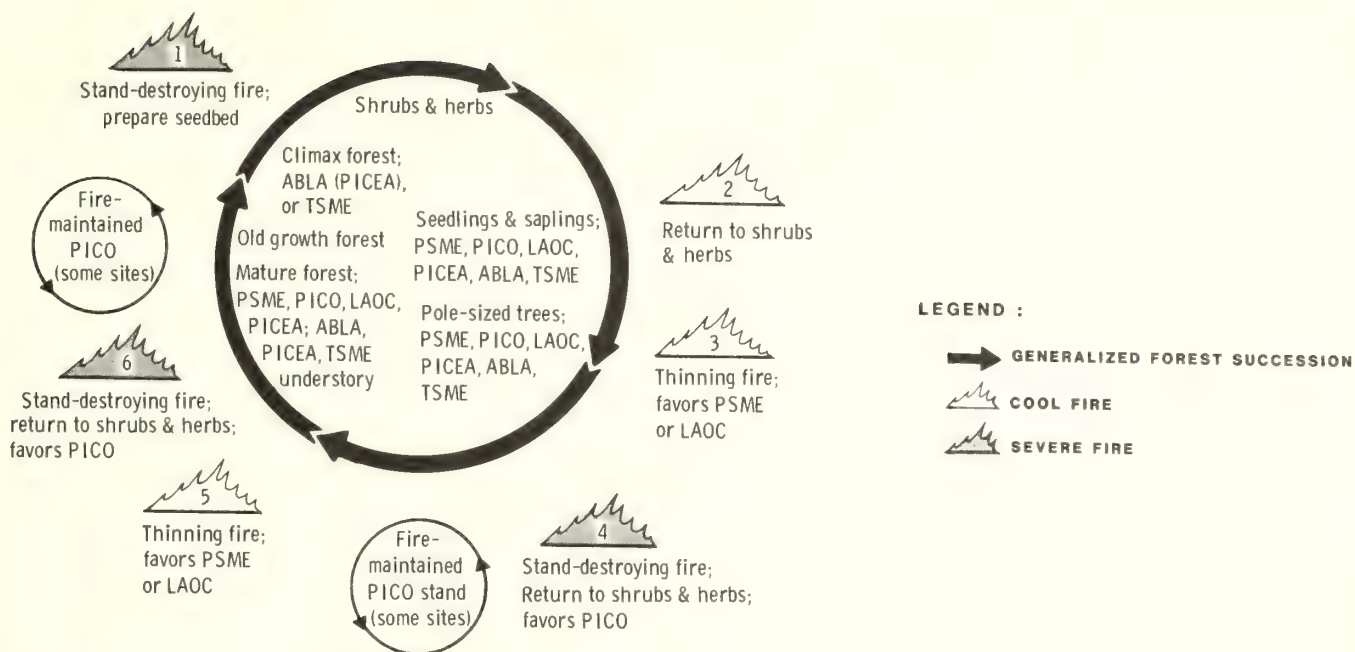


Figure 32—Generalized forest succession in Fire Group Eight: dry, lower subalpine habitat types. And in Fire Group Nine: moist, lower subalpine habitat types.

Available evidence indicates that fires on such sites are infrequent and are mostly low severity or stand-replacing. Moderate-severity fires are apparently less frequent although they do occur (Sneck 1977). Pathways illustrating successional events (fig. 33) following low or severe fires should be considered more applicable to Fire Group Nine than to Fire Group Eight.

Many stands belonging to the PICEA/EQAR h.t. do not follow the successional pathways shown for other Fire Groups Eight and Nine habitat types (fig. 33). On these sites, spruce is the only conifer in seral and climax conditions. Such stands may tolerate some low-severity fire, but

in most cases, any fire will return them to the shrub/herb stage. Some sites will have substantial amounts of aspen or black cottonwood in seral stands. Without periodic fire these intolerant trees are replaced by the tolerant longer lived spruce. With fire, aspen may be dominant because of its ability to regenerate from root suckers.

The successional sequences of community types and accompanying information provided by Arno and others (1985) can be used as an aid for predicting successional development of seral communities (and treatment response) within the ABLA/MEFE h.t. in relation to various types of fire and harvest treatments.

The flowchart illustrates the Wisconsin Forest Succession Model, showing 17 states and the transitions between them based on disturbance severity and type.

States:

- 1: Shrub & herbs
- 2: Seedlings & saplings: PSME, PIPO, PICEA & ABLA
- 3: C. (Poles, PSME, PICE, PICEA & ABLA)
- 4: Mature forest: PSME, PICE, PICEA & ABLA
- 5: Near climax: PICEA & ABLA; some PSME, PICEA & ABLA understorey
- 6: Old-growth forest: PICEA & ABLA
- 7: Open PSME forest, some PIPO, PICEA regens.
- 8: Open PSME forest, some PIPO, PICEA understorey; mixed regens.
- 9: Old-growth forest: some PIPO, PICEA, PSME, mixed understorey
- 10: Open PSME forest, some PIPO, PICEA regens.
- 11: Open, old-growth PSME, mostly PSME regens.
- 12: Open PSME forest, some PIPO, PICEA regens.
- 13: Open PSME forest, some PIPO, PICEA regens.
- 14: Open PSME forest, some PIPO, PICEA regens.
- 15: Open PSME forest, some PIPO, PICEA regens.
- 16: Open PSME forest, some PIPO, PICEA regens.
- 17: Old-growth forest: some PIPO, PICEA, PSME, mixed understorey

Transitions:

- 1 to 2: Any
- 2 to 3: Low-severity
- 3 to 4: Severe
- 4 to 5: Low
- 5 to 6: Mod.-severe
- 6 to 1: Low
- 6 to 2: Any
- 6 to 3: Low-severity
- 6 to 4: Severe
- 6 to 5: Mod.-severe
- 6 to 6: Low
- 6 to 7: Low
- 6 to 8: Low
- 6 to 9: Low
- 6 to 10: Low
- 6 to 11: Low
- 6 to 12: Low
- 6 to 13: Low
- 6 to 14: Low
- 6 to 15: Low
- 6 to 16: Low
- 6 to 17: Low
- 7 to 8: Low
- 8 to 9: Low
- 9 to 10: Low
- 10 to 11: Low
- 11 to 12: Low
- 12 to 13: Low
- 13 to 14: Low
- 14 to 15: Low
- 15 to 16: Low
- 16 to 17: Low
- 17 to 1: Low
- 17 to 2: Any
- 17 to 3: Low-severity
- 17 to 4: Severe
- 17 to 5: Mod.-severe
- 17 to 6: Low
- 17 to 7: Low
- 17 to 8: Low
- 17 to 9: Low
- 17 to 10: Low
- 17 to 11: Low
- 17 to 12: Low
- 17 to 13: Low
- 17 to 14: Low
- 17 to 15: Low
- 17 to 16: Low
- 17 to 17: Low

The diagram illustrates the succession of vegetation communities in the Białowieża National Park, showing the progression from initial communities (A, B, C) through various stages (D, E, F) to a climax (F), influenced by fire frequency and severity.

Communities and their components:

- A:** herbs, shrubs
- B:** Sekelins & saplings, LACC, PSME, PICEA, TSME, POME, or ABLA & PICEA
- C:** PICEA, LACC, PSME, PICEA, POME, TSME, or ABLA
- D:** PICEA, LACC, PSME, PICEA, POME, TSME, or ABLA
- E:** near climax; mostly PICEA, ABLA, TSME, some PSME, LACC, few PICEA
- F:** Climax; ABLA, PICEA or TSME

Succession paths and fire influence:

- Succession in absence of fire (solid arrows):** A → B → C → D → E → F.
- Response to fire (dashed arrows):**
 - Low (cool or light surface fire):** A → B, B → C, C → D, D → E, E → F.
 - Low-mod. (fire of moderate severity):** B → C, C → D, D → E, E → F.
 - Moderate-severe:** C → D, D → E, E → F.
 - Severe or repeated fires:** D → E, E → F.
- Self-reinforcing loops (dashed arrows with circles):**
 - Low-mod.:** D → D, E → E, F → F.
 - Low:** F → F.

LEGEND :

- Solid arrow:** SUCCESSION IN ABSENCE OF FIRE
- Dashed arrow:** RESPONSE TO FIRE
- LOW:** COOL OR LIGHT SURFACE FIRE
- MOD.** FIRE OF MODERATE SEVERITY
- SEVERE:** HOT STAND-REPLACEMENT FIRE
- 1, 2, etc. REFERENCE NUMBER (SEE TEXT)**

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Fire Management Considerations

Fire protection is usually necessary in undisturbed stands during severe burning conditions. This is especially true for areas where timber production is a management objective. When burning conditions are less than severe, fires may be of low to moderate severity and result in only moderate damage or no damage to overstory trees (other than subalpine fir), despite the relatively low fire resistance of many of the species present. If slash is present, unacceptable tree mortality can result even during moderate burning conditions.

Broadcast burning is an effective method for reducing slash hazards and for preparing seedbeds in clearcuts and in larch/Douglas-fir shelterwoods. Timing of a burn is important. These sites are so cool and moist that times when effective broadcast burns can be achieved are limited. The moisture content of the duff must be low enough to allow the fire to bare mineral soil over much of the area. Often, such favorable moisture conditions occur only during the late summer. When prescribed fires are conducted under high duff moisture conditions, failure to adequately bare mineral soil often results in establishment of a shrubfield, especially on north slopes. Shearer and Schmidt (1982) describe how a shrubfield that resulted from an unsuccessful burn was successfully prescribe burned and reforested 14 years later.

Burning slash in large windrows or piles can create enough heat to alter the physical structure of the soil, which in turn may result in a reduction in density and growth rate of conifer regeneration. Such a condition may persist for 15 years or more (Vogel and Ryder 1969). Consequently, windrows should be narrow and piles should be small when these methods are used.

Additional guidelines for fire use for slash disposal and site preparation and silviculture are provided by Roe and others (1970). This reference should be consulted before planning fire use on these sites.

Slash disposal plans should consider the need for some residues to remain on the site for nutrient cycling and as a source of shade for successful seedling development.

The often complex structure of subalpine forests reflects their fire history. These forests are what they are partly because of past patchy or uneven burns and partly because of their climate and soils. As a general rule, their natural development has not been affected by past fire suppression (Habeck and Mutch 1973). Management objectives are oriented toward nonconsumptive use such as watershed and big game sanctuary. Many are roadless; many are within designated wildernesses. Consequently, the appropriate fire management policy may be one that allows some fires to burn according to a predetermined fire management prescription (Fischer 1984).

FIRE GROUP TEN: COLD, MOIST UPPER SUBALPINE AND TIMBERLINE HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
Upper Subalpine		
820	<i>Abies lasiocarpa</i> - <i>Pinus albicaulis</i> / <i>Vaccinium scoparium</i> h.t. (ABLA-PIAL/VASC), subalpine fir-whitebark pine/grouse whortleberry	West central
831	<i>Abies lasiocarpa</i> / <i>Luzula hitchcockii</i> h.t.- <i>Vaccinium scoparium</i> phase (ABLA/LUHI-VASC), subalpine fir/smooth woodrush-grouse whortleberry phase	Northwestern and west central
832	<i>Abies lasiocarpa</i> / <i>Luzula hitchcockii</i> h.t.- <i>Menziesia ferruginea</i> phase (ABLA/LUHI-MEFE), subalpine fir/smooth woodrush-menziesia phase	Northwestern and west central
841	<i>Tsuga mertensiana</i> / <i>Luzula hitchcockii</i> h.t.- <i>Vaccinium scoparium</i> phase (TSME/LUHI-VASC), mountain hemlock/smooth woodrush-grouse whortleberry phase	Northwestern
842	<i>Tsuga mertensiana</i> / <i>Luzula hitchcockii</i> h.t.- <i>Menziesia ferruginea</i> phase (TSME/LUHI-MEFE), mountain hemlock/smooth woodrush-menziesia phase	Northwestern
Timberline		
850	<i>Pinus albicaulis</i> - <i>Abies lasiocarpa</i> h.t.'s (PIAL-ABLA h.t.'s), whitebark pine-subalpine fir	Northwestern and west central
860	<i>Larix lyallii</i> - <i>Abies lasiocarpa</i> h.t.'s (LALY-ABLA h.t.'s), subalpine larch-subalpine fir	Northwestern and west central
870	<i>Pinus albicaulis</i> h.t.'s (PIAL h.t.'s), whitebark pine	West central

Vegetation

Fire Group Ten consists of high-elevation forests near and at the timberline. All the stands lie above the climatic limits of Douglas-fir, and many stands are above the cold limits of lodgepole pine. Subalpine fir or mountain hemlock are the indicated climax in all of the upper subalpine habitat types in western Montana. Whitebark pine and Engelmann spruce are long-lived seral species. Lodgepole pine occurs on some upper subalpine sites.

Timberline habitat types support stands composed of subalpine larch, whitebark pine, Engelmann spruce, and subalpine fir. Trees characteristically grow in groups with open areas in between. Competition due to differences in tolerance is not as pronounced at timberline as it is in lower forests. Habitat types at these high elevations are named for their dominant tree component rather than an indicated climax species.

Undergrowth in the upper subalpine habitat types is usually composed of only a few important species, and in timberline habitat types undergrowth occurs in mosaics. Shrubs that may occur on Group Ten sites include menziesia, red heath, yellow mountain heather, white flower rhododendron, mountain gooseberry, grouse whortleberry, and common juniper.

Common forbs are broadleaf arnica, ballhead sandwort, beargrass, and slender hawkweed. Grass and grasslike vegetation include Ross sedge, Idaho fescue, Parry rush, and smooth woodrush.

Forest Fuels

Fire Group Ten sites are characterized by relatively sparse fine fuels and moderate to heavy loadings of widely scattered large-diameter fuels. Brown and See (1981) report an average downed woody loading of about 18 tons per acre (about 4 kg/m²) for stands in western Montana (table 6).

Fuel inventory data for subalpine and timberline forests are scarce. Data collected on several Selway-Bitterroot Wilderness sites are shown in table 14.

The fuel loadings shown in table 14 are averages for all sampled stands. They differ, therefore, from the individual stand data presented for the other Fire Groups. Keep in mind that the standard deviations of table 14 values are often as great as the values themselves. Nonetheless, trends are apparent. The drier ABLA/LUHI-VASC h.t.

yields, on the average, about a third the amount of down and dead woody material as the moist ABLA/LUHI-MEFE h.t. Also notice the additional amount of fuel produced by the duff within these habitat types. Inspection of the original data sheets shows that much of the down woody material 3 inches (8 cm) and larger is rotten.

The downed and dead woody fuel loadings often take the form of scattered large-diameter downfall resulting from wind and snow breakage, windthrow, and mortality caused by insects or disease. Such heavy fuels do not necessarily reflect a serious fire hazard. The mitigating effects of the normally cool, moist site, the short fire season, and the usually sparse and often discontinuous nature of fine surface fuels must be considered when evaluating overall fire potential. Examples of Group Ten fuel and stand conditions are shown in figure 34.

Role of Fire

Fire is secondary to site factors (climate and soil) as an influence on forest development on these sites. The cold, moist, rocky, snowbound, unproductive, and otherwise fire-resistant environment that characterizes many of the sites not only makes fires infrequent but severely limits their areal extent. Lightning does ignite fires, but the paucity of continuous fine surface fuels coupled with the rain that commonly accompanies thunderstorms usually limits fire spread and severity. Historical fire frequencies ranging from 35 to 300 years have been reported for individual sites (Romme 1980). Such figures are difficult to interpret because a fire may involve only one or two trees in a stand. For this reason the concept of fire frequency does not apply well in upper subalpine and timberline sites.

In more continuous forests of this group, the most pronounced fire effect is to produce stand-replacing fires at long intervals, perhaps 200 years or more. Stand-destroying fires are most likely to occur during extended drought conditions when severe wind-driven crown fires develop in the forests below and burn into the upper subalpine and timberline forests. Vegetation recovery following such fires is usually slow because of the extremely short growing season and cold climate. Arno (1984) reported reinvasion of whitebark pine on timberline sites 50 to 200 years after fire in the Bitterroot Mountains. Based on his observations in many upper subalpine habitat types, Arno (1986) suggests that fire has been important in perpetuating an abundance of whitebark pine.

Table 14—Average fuel loadings for several Group Ten stands in western Montana

Stand number	Habitat type-phase	Duff depth	Size class (inches)							Total
			0-1/4	1/4-1	1-3	3-6	6-10	10-20	20+	
		<i>Inches</i>	<i>Tons/acre</i>							
80	ABLA/LUHI-VASC	7.2	0.2	0.7	0.2	0.7	3.3	2.8	0	7.0
48	ABLA/LUHI-MEFE	33.5	.2	.6	1.4	1.9	7.0	11.1	3.6	25.8
25	LALY-ABLA	11.2	.1	.3	.1	.4	2.0	4.8	3.3	11.0



A



B



C



D



E

Figure 34—Examples of fuel and stand conditions in some Fire Group Ten habitats. (A) A PIAL-ABLA h.t. with scattered downed woody fuel and flammable thicket of fir. Snags shown will eventually add to surface fuel loads. (B) A PIAL h.t. with sparse surface fuels and clusters of whitebark pine. (C) An ABLA/LUHI h.t. showing lush surface vegetation and low-hanging branches. (D) An ABLA/LUHI-MEFE h.t. with heavy dead woody fuels intermingled with dense live fuels. (E) A typical LALY-ABLA h.t.

Forest Succession

Secondary succession begins with a mixture of herbs and shrubs (fig. 35). It is likely that herbaceous plants will dominate for an extended period. Fire may initiate secondary succession, but it is unlikely that it has a role in maintaining it. Physical disruption of the stand by snow and wind, rock slides, and talus slippage is more important on moist sites and north slopes than is fire in maintaining early stages of succession.

It takes a long time before conifers dominate some sites, perhaps 100 years. It may take another 100 years before a mature forest exists. It is unlikely that fuel or stand conditions will support a fire of any consequence during this period. Surface fires do occur, especially in whitebark pine stands on south slopes and ridges. Such fires act as underburns, reducing fuels and killing some overstory trees. Severe fires may occur over small areas, but their effect will usually be limited to the creation of vegetative mosaics. Eventually the mature forest will begin to break up under the impact of wind and snow breakage, windthrow, mortality caused by insects and disease, and senescence. Stand-destroying fires, especially those that invade from lower elevation forests, become a possibility during extended drought.

Without disturbance, the mature trees will progress into a climax stand. This advance successional stage requires decades, possibly two or three centuries. Low- to moderate-severity fires rarely have a significant impact on a mature stand because of the open structure and lack of continuous fine woody fuels. However, severe fires that enter the crowns and kill the cambium of trees return the site to the early successional stages (fig. 35).

A simple succession pathway postulated for Fire Group Ten is shown in figure 36.

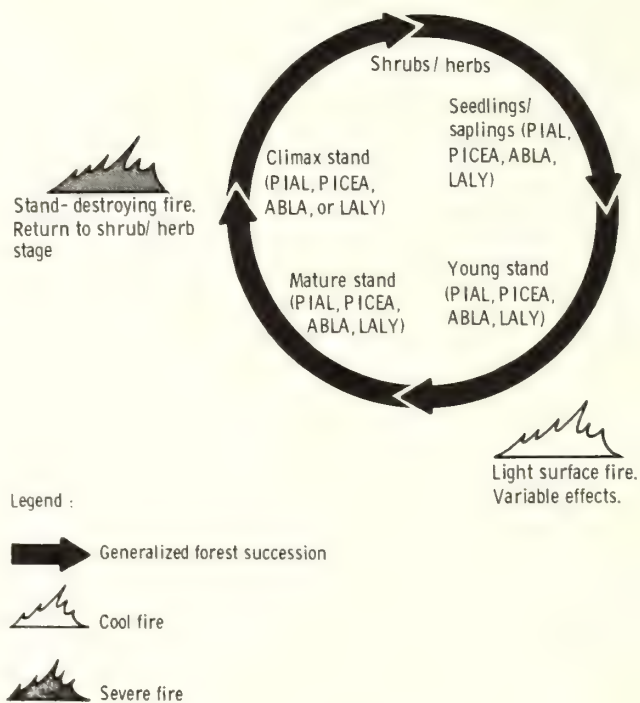


Figure 35—Generalized forest succession in Fire Group Ten: cold, moist upper subalpine and timberline habitat types. Low-severity lightning fires may occur at any stage with little effect on succession.

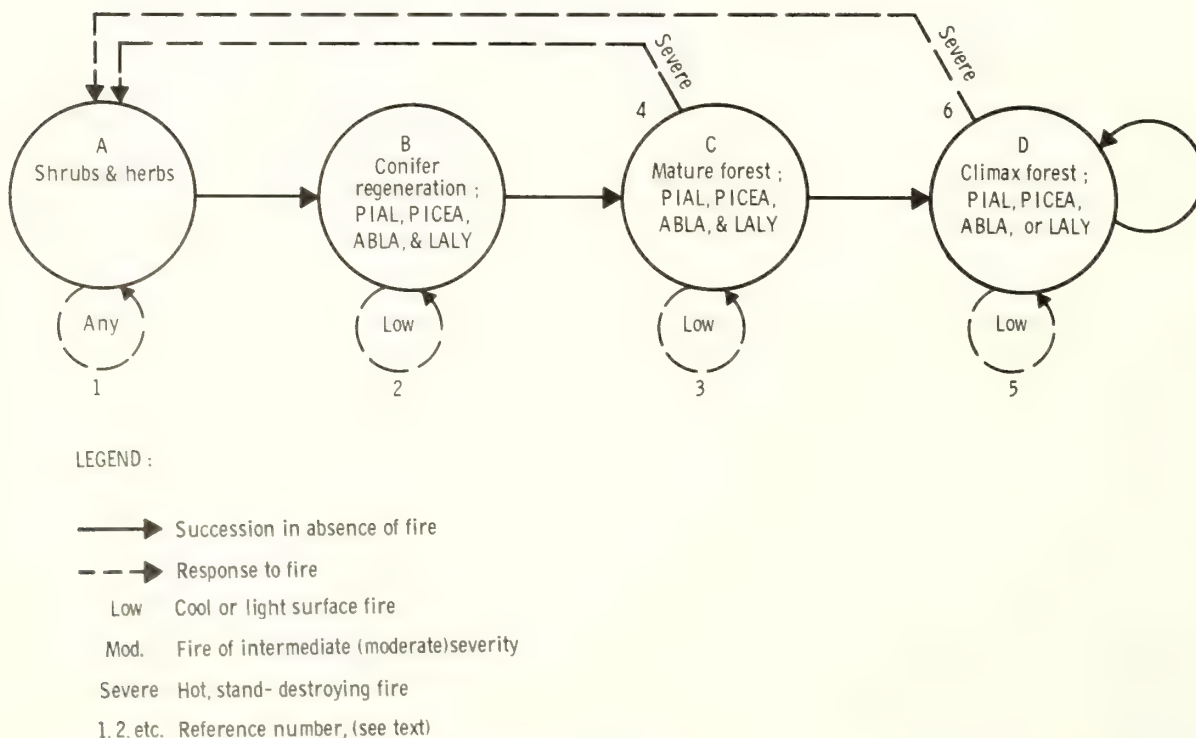


Figure 36—Hypothetical fire-related successional pathways for Fire Group Ten habitat types.

Fire Management Considerations

Timber production is rarely an important management objective for forests in this group. Most areas are managed as watersheds, natural areas, and sanctuaries for wildlife. For example, whitebark pine forests are important food producers for jays, bears, squirrels, deer, and elk (Forcella and Weaver 1980). Most are roadless, and many are in designated wildernesses. Fire is an infrequent visitor, and when it does occur, damage in terms of management objectives is generally slight. But these sites are often fragile and can easily be damaged by modern, mechanized firefighting equipment.

The status of whitebark pine communities should be of particular concern to managers of upper subalpine forests. In some areas the welfare of the grizzly bear, a threatened species, appears to be partially dependent on the availability of whitebark pine cone crops in large caches made by red squirrels (Arno 1986). On many upper subalpine sites whitebark pine is being replaced successionally by more shade-tolerant species. Arno (1986) attributes this situation to fire suppression coupled with damage from mountain pine beetle and white pine blister rust (*Cronartium ribicola*). Due to the wilderness location of many whitebark pine stands, fire may be the major practical means of regenerating this species. Consequently, the primary fire management consideration for many upper subalpine and timberline forests should be the aggressive development of prescriptions that allow fire to more nearly play its natural role.

FIRE GROUP ELEVEN: WARM, MOIST GRAND FIR, WESTERN REDCEDAR, AND WESTERN HEMLOCK HABITAT TYPES

ADP code	Habitat type-phase (Pfister and others 1977)	Montana forest region (Arno 1979)
510	<i>Abies grandis/Xerophyllum tenax</i> h.t. (ABGR/XETE), grand fir/beargrass	Northwestern and west central
521	<i>Abies grandis/Clintonia uniflora</i> h.t.- <i>Clintonia uniflora</i> phase (ABGR/CLUN-CLUN), grand fir/queencup beadlily-queencup beadlily phase	Northwestern and west central
522	<i>Abies grandis/Clintonia uniflora</i> h.t.- <i>Aralia nudicaulis</i> phase (ABGR/CLUN-ARNU), grand fir/queencup beadlily-wild sarsaparilla phase	Northwestern and west central
523	<i>Abies grandis/Clintonia uniflora</i> h.t.- <i>Xerophyllum tenax</i> phase (ABGR/CLUN-XETE), grand fir/queencup beadlily-beargrass phase	Northwestern

591	<i>Abies grandis/Linnaea borealis</i> h.t.- <i>Linnaea borealis</i> phase (ABGR/LIBO-LIBO), grand fir/twinflower-twinflower phase	Northwestern and west central
592	<i>Abies grandis/Linnaea borealis</i> h.t.- <i>Xerophyllum tenax</i> phase (ABGR/LIBO-XETE), grand fir/twinflower-beargrass phase	Northwestern
531	<i>Thuja plicata/Clintonia uniflora</i> h.t.- <i>Clintonia uniflora</i> phase (THPL/CLUN-CLUN), western redcedar/queencup beadlily-queencup beadlily phase	Northwestern and west central
532	<i>Thuja plicata/Clintonia uniflora</i> h.t.- <i>Aralia nudicaulis</i> phase (THPL/CLUN-ARNU), western redcedar/queencup beadlily-wild sarsaparilla phase	Northwestern and west central
533	<i>Thuja plicata/Clintonia uniflora</i> h.t.- <i>Menziesia ferruginea</i> phase (THPL/CLUN-MEFE), western redcedar/queencup beadlily-menziesia phase	Northwestern and west central
550	<i>Thuja plicata/Oplodanax horridum</i> h.t. (THPL/OPHO), western redcedar/devil's club	Northwestern
571	<i>Tsuga heterophylla/Clintonia uniflora</i> h.t.- <i>Clintonia uniflora</i> phase (TSHE/CLUN-CLUN), western hemlock/queencup beadlily-queencup beadlily phase	Northwestern
572	<i>Tsuga heterophylla/Clintonia uniflora</i> h.t.- <i>Aralia nudicaulis</i> phase (TSHE/CLUN-ARNU), western hemlock/queencup beadlily-wild sarsaparilla phase	Northwestern

Vegetation

Fire Group Eleven is composed of moist, warm habitat types often occurring on valley bottoms, benches, ravines, and protected exposures in west-central Montana and more commonly on upland sites in northwestern Montana. This group occurs only west of the Continental Divide in Montana and reflects the influence of the inland maritime climate in west-central and northwestern portions of the State.

Up to 10 species of conifers may occur during the successional process: ponderosa pine, Douglas-fir, Engelmann spruce, lodgepole pine, subalpine fir, grand fir, western redcedar, western white pine, western larch, or western hemlock. The potential establishment of any of these species depends on site conditions, fire frequency, and the availability of viable seed. Western hemlock, western redcedar, and grand fir are climax species within the group.

Undergrowth is characterized by a rich variety of moist site herbs and shrubs. Important shrubs include western serviceberry, common snowberry, thimbleberry, white spirea, bunchberry dogwood, dampwoods blueberry (blue huckleberry), mountain lover, Rocky Mountain maple, and menziesia. Pacific yew and devil's club are locally common. Widespread moist site forbs are darkwoods violet, queen-cup beadlily, common beargrass, sidebells shineleaf, broad-leaf arnica, starry false Solomon's seal, wild sarsaparilla, American trailplant, American twinflower, western rattlesnake plantain, lady fern, wartberry fairybells, and three-leaf foamflower. Columbia bromegrass, pinegrass, and elk sedge are the predominant graminoid species.

Forest Fuels

Fuel loadings average 25 tons per acre (5.6 kg/m²), which exceeds that of any other Fire Group in western Montana. Much of the downed woody fuel results from

accumulated deadfall and occasional natural thinning. Because of the often heavy grand fir and cedar component, a relatively heavy load of twigs and small branchwood is usually included in the fuel load. Compared to the other Fire Groups, Group Eleven fuel loadings average higher in all size classes (table 6). The large material, which may account for 75 percent of the fuel load, is often rotten.

Despite the heavy fuel loadings that characterize these stands, fire hazard is normally low to moderate under normal weather conditions. The potential for serious conflagrations is usually mitigated by the high humidity of these moist sites. Young stands and older open-canopy stands often support a lush undergrowth, while closed-canopy stands allow little sunlight to reach the cool, moist forest floor. Characteristic stand and fuel conditions are shown in figures 37, 38, and 39 for grand fir sites, western redcedar sites, and western hemlock sites, respectively. Fuel loadings are presented in table 15.



Figure 37—Characteristic stand and fuel conditions for Fire Group Eleven grand fir habitat types. Stand 63 is an ABGR/XETE h.t., others are ABGR/CLUN-CLUN. Stand age and fuel loadings are given in table 15.



E



F



G

Figure 37—(Con.)



A



B



C



D

Figure 38—Characteristic stand and fuel conditions for Fire Group Eleven western redcedar habitat types. Stand 17A is a THPL/CLUN-ARNU h.t. Stands 6A and 7A are THPL/CLUN-CLUN h.t.'s. And stand 15A is an old growth cedar stand on a THPL/OPHO h.t. Stand age and fuel loadings are given in table 15.



A



B



C



D



E

Figure 39—Characteristic stand and fuel conditions for Fire Group Eleven western hemlock habitat types. All of these stands are on TSHE/CLUN-CLUN h.t.'s. Stand age and fuel loadings are given in table 15.

Table 15—Fuel loadings by size class for stands shown in figures 37, 38, and 39

Stand number	Habitat type-phase	Age ¹	Duff depth	Size class (inches)							Total
				0-1/4	1/4-1	1-3	3-6	6-10	10-20	20 +	
		<i>Years</i>	<i>Inches</i>	<i>Tons/acre</i>							
9A	TSHE/CLUN-CLUN	170	2.8	0.4	1.1	0.5	1.8	4.6	0.5	0	8.9
4A	TSHE/CLUN-CLUN	120	2.0	.6	1.2	1.3	4.0	2.8	1.0	0	10.9
17A	THPL/CLUN-ARNU	100	3.1	.2	1.1	2.3	2.1	2.9	2.9	0	11.5
12A	ABGR/CLUN-CLUN	115	2.7	.3	1.1	.4	1.1	6.4	3.5	0	12.8
3A	TSHE/CLUN-CLUN	190	2.9	.4	1.1	1.5	1.8	4.1	4.4	0	13.3
16	ABGR/CLUN-CLUN	120	2.6	.9	1.7	2.1	3.3	6.1	2.2	0	16.3
6A	THPL/CLUN-CLUN	200	3.1	.4	1.7	1.1	2.2	2.8	4.2	4.6	17.0
7A	THPL/CLUN-CLUN	210	3.5	.4	1.7	3.2	1.7	7.9	4.6	0	19.5
13	ABGR/CLUN-CLUN	100	1.8	.3	1.5	3.5	9.3	5.0	2.6	0	22.2
63	ABGR/XETE	125	1.9	.4	1.9	.7	3.6	8.3	7.4	0	22.3
65	ABGR/CLUN-CLUN	120	2.6	.5	1.9	3.6	7.2	10.8	0	0	24.0
8A	TSHE/CLUN-CLUN	210	3.0	.7	2.1	3.1	5.4	3.9	7.8	4.1	27.1
16A	TSHE/CLUN-CLUN	85	5.3	.6	2.2	2.5	9.3	21.1	3.2	0	29.9
25	ABGR/CLUN-CLUN	115	4.0	1.1	2.2	5.5	.6	6.3	17.1	2.6	35.4
66	ABGR/CLUN-CLUN	280	4.0	.6	1.6	1.2	3.5	4.4	26.7	0	38.0
15A	THPL/OPHO	400 +	2.8	.2	1.1	1.0	.4	1.3	3.2	50.4	57.6

Role of Fire

The inland maritime climate that prevails in northwestern Montana exerts a strong influence on forest development and the role of fire in these forests.

The relatively warm, moist conditions sustain the growth of diverse and highly productive stands. These same factors keep the fire frequency generally low. Hydric and mesic sites may actually serve as firebreaks to ground fires. A fire may burn into the edge of a stand, possibly scarring some trees, but it will usually die out when it reaches the moist duff layer.

Moist weather conditions predominate, but the region is occasionally subject to severe summer drought. Heavy fuel loadings exist in most stands because of overall high plant productivity. This, combined with droughty conditions, sets the stage for severe, widespread fires. Stands are replaced and sites revert to pioneer species.

Fire severities vary greatly from the minor ground fire of moist sites to the stand replacement fire. Within this range of variation, some generalities can be made. In Group Eleven habitat types, fire can:

1. Provide mineral seedbed suitable for both seral and potential climax species.
2. Produce a mosaic of various seral communities across the landscape.

3. Affect within-stand tree diversity because of differential species response to the fire regime.

When considering the role of fire in Group Eleven, remember that there is a vast site and moisture difference between dry grand fir (ABGR/XETE) habitat types and the wet cedar and hemlock (THPL/OPHO) habitat types.

Fire frequencies for cedar-hemlock stands in northern Idaho have been estimated by Arno and Davis (1980). They reported fire-free intervals from 50 to greater than 200 years. Within the ABGR/CLUN h.t. in the Swan Valley, Antos and Habeck (1981) estimated a mean fire-free interval of 100 to 200 years between stand-replacing fires. Perhaps the 30-year interval reported within the ABGR/CLUN h.t. in the Swan Valley (Freedman and Habeck 1985) represents the extreme for these forests.

Postfire succession is governed by more than the nature of the fire itself. Fires of the same severity in the cedar-hemlock zone may result in different seral communities. The initial floral component, seeds stored on site, and the accidents of natural seeding and seedling establishment, may structure the community following the fire more than the characteristics of the fire itself. While this is generally true for all Fire Groups, it is more pronounced in Fire Group Eleven.

Forest Succession

The theoretical climax condition is a reproducing stand of grand fir, western hemlock, or western redcedar, as shown in figure 40 (subsequent numbers in this section refer to fig. 40).

Following a stand-replacing fire, succession begins with a shrub/herb field. Duration of this stage depends on the availability of tree seed and the occurrence of multiple burns (No. 1). Many sites in northern Idaho initially burned in 1910 and subsequently reburned in the 1920's and 1930's remain as shrub/herb fields today.

If seed is available and multiple burns do not occur, seedlings of both climax and seral trees will establish on a burned site (No. 2). Most fires in the seedling/sapling stage will revert the stand to a treeless condition (No. 3).

Moisture is not generally limiting in stands included in Fire Group Eleven. These sites are highly productive, and pole and mature stands are usually dense. Although this condition leads to a high fuel loading, severe fires are infrequent because of the high moisture status.

Low to moderate fires (No. 4) in pole-sized or mature

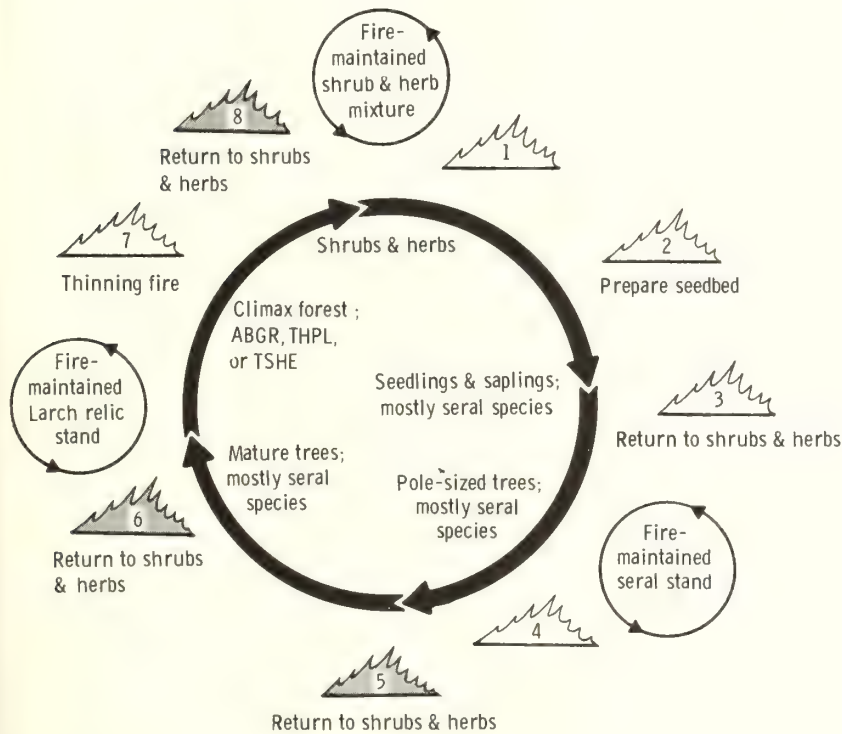
stands favor intolerant seral species over climax western redcedar, grand fir, or western hemlock, which are less fire resistant.

When severe fires do occur in these stands (No. 5) they are generally returned to a shrub/herb field. This may be a short-lived condition if serotinous lodgepole pine was present in the preburn stand. In this case, seedlings of lodgepole pine would soon initiate a new stand.

Mature larch may survive severe fires in mature or near-climax stands (No. 6). These trees would then provide seed for a postburn stand. A "larch relict" stand may be the result of frequent low to moderate fires in mature stands.

True climax status, where grand fir or western hemlock or western redcedar or a combination are the only trees on site, is rarely achieved. Seral species are long-lived, and fire occurs frequently enough that stands seldom develop beyond the near-climax stage.

Climax stands may withstand low thinning fires (No. 7), but moderate or severe fires (No. 8) return the site to a shrub/herb stage.



LEGEND :

- GENERALIZED FOREST SUCCESSION
- ~ COOL FIRE
- ~ SEVERE FIRE

Figure 40—Generalized forest succession in Fire Group Eleven: moist, warm grand fir, western redcedar, and western hemlock habitat types.

Habeck (1963, 1968, 1970) has studied the composition and successional development of Glacier National Park cedar-hemlock forests. Figure 41 depicts his generalized scheme of fire's impact on succession in these forests. Figure 42 presents generalized successional pathways that are hypothesized to be significant in Swan Valley, Flathead National Forest, grand fir forests following stand-replacing fires (Antos and Habeck 1981; Antos and Shearer 1980).

In the hypothetical successional pathway presented in figure 43, two general sequences are illustrated: (1) the circumstance in which lodgepole pine has the major role in early stand development, and (2) where larch becomes the dominant seral species.

There are three relatively dry grand fir habitat types in western Montana: ABGR/XETE h.t., ABGR/LIBO-XETE h.t., and ABGR/LIBO-LIBO h.t. Stands within these types undergo a postdisturbance successional sequence that fits the general pattern illustrated in the multiple pathway diagram (fig. 43). However, their fire ecology differs enough to warrant individual discussion. Compared with other habitat types in this Fire Group, they (1) have a greater fire frequency, (2) experience more underburning

and fewer stand replacing fires, and (3) tend to be dominated by seral species, with grand fir playing a minor role in early successional stands.

The relatively dry conditions permit a higher frequency of low- or moderate-severity fires that in turn favor ponderosa pine, lodgepole pine, larch, and Douglas-fir over the less resistant grand fir. Arno and Petersen (1983) estimated a mean fire interval of 30 years for grove-sized stands within the ABGR/LIBO-LIBO h.t. sites in the Bitterroot Valley of western Montana. This can be compared with the considerably longer estimates for more mesic types (discussed under "Role of Fire" for Group Eleven habitat types).

The ABGR/XETE h.t. is the driest of all the grand fir habitat types represented in Montana. Lodgepole pine or larch or both are the important successional species in this type, with lodgepole pine dominating. The likelihood of stand-replacing fires within the ABGR/XETE h.t. during presettlement times was less than that of other Group Eleven habitat types because of their lower productivity and more frequent underburning. The portions of multiple pathway sequence 1 (fig. 43) that illustrate succession after low or moderate fires are better models of postfire

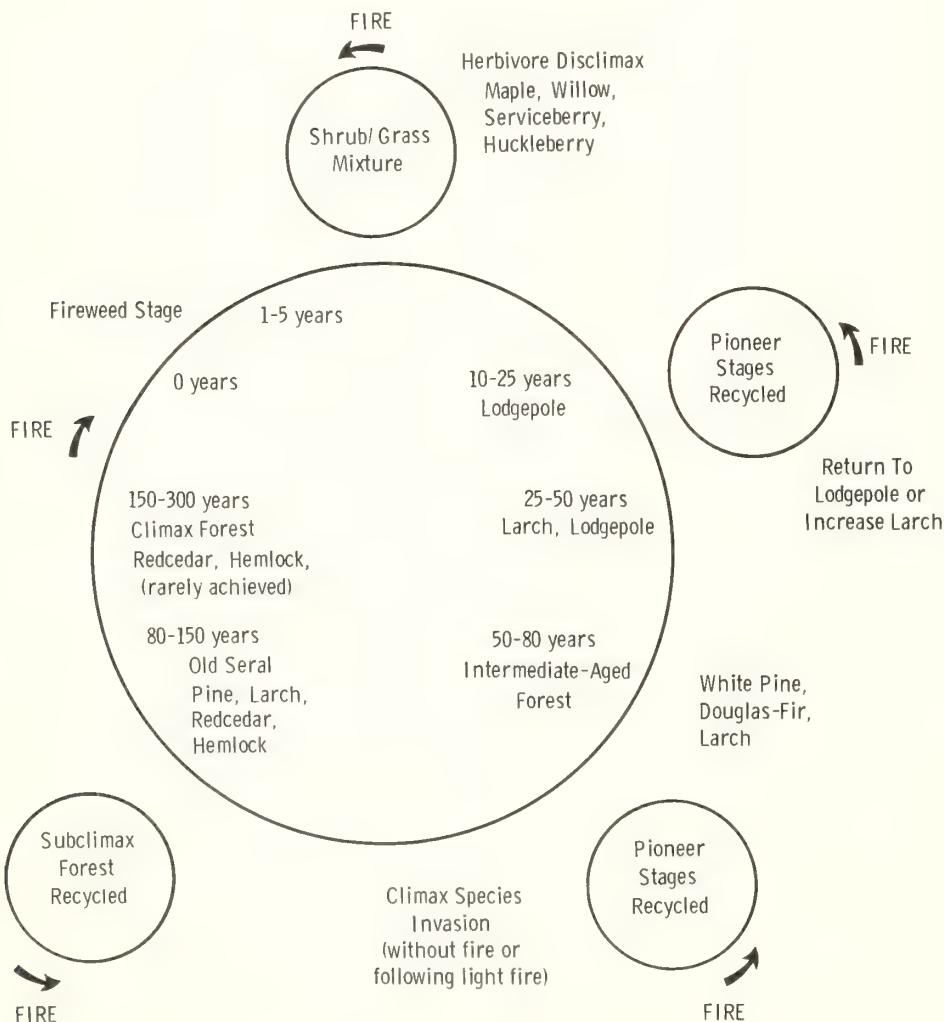


Figure 41—The effect of fire on successional development in upland cedar-hemlock forests near Lake McDonald, Glacier National Park, MT (after Habeck 1970).

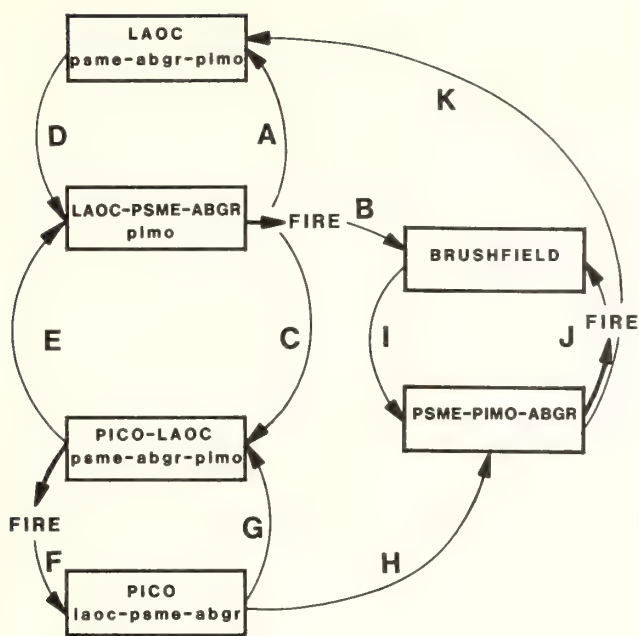


Figure 42—Patterns of community dynamics within the Swan Valley, Flathead National Forest, MT. (A) Lodgepole pine seed source absent. (B) Larch and lodgepole establishment fail. (C) Lodgepole seed source present. (D) Douglas-fir and grand fir increase with time. (E) Lodgepole dies out of the stand. (F) Burned stand young enough that larch does not survive fire so lodgepole increases. (G) Lodgepole discussion. (H) Lodgepole dies out and no larch in stand. (I) Slow brushfield invasion. (J) No larch seed source present. (K) Larch seed source present. (After Antos and Habeck 1981.)

tree response for stands within the drier ABGR/XETE h.t. than those for severe fires.

In presettlement times western larch was also an important seral species on sites within the ABGR/LIBO-XETE h.t. and ABGR/LIBO-LIBO h.t. In some of these stands, especially those within the ABGR/LIBO-LIBO h.t., larch shared the role of seral dominant with ponderosa pine. These two trees occurred together in varying proportions. Stand composition ranged from larch dominated, to mostly ponderosa pine. On all stands, the tolerant understory consisted of Douglas-fir and grand fir. Succession with ponderosa pine is similar to that for larch. Successional pathway 2 (fig. 43) models the process.

Fire Management Considerations

Fire Group Eleven habitat types are often highly productive timber-growing sites. Where timber management is the objective, and even-aged silviculture is applied to favor seral species such as ponderosa pine or overstory Douglas-fir and western larch, broadcast fire can be used to reduce slash hazard and prepare seedbed after harvest operations. Broadcast burning is inappropriate when partial cutting leaves heat-susceptible grand fir, western white pine, and associated species in the overstory. Recommended silvicultural procedures, including the use of fire, to obtain natural regeneration within the ABGR/CLUN h.t. in the Swan Valley are summarized in table 16 (Antos and Shearer 1980). On most sites within the THPL/CLUN h.t., according to Antos and Shearer (1980), the procedure (table 16) recommended for mature forest on north or east slopes with larch can be used. They also recommend a shelterwood cut with broadcast burning or scarification and piling and burning for south slope seepage sites within the THPL/CLUN h.t.

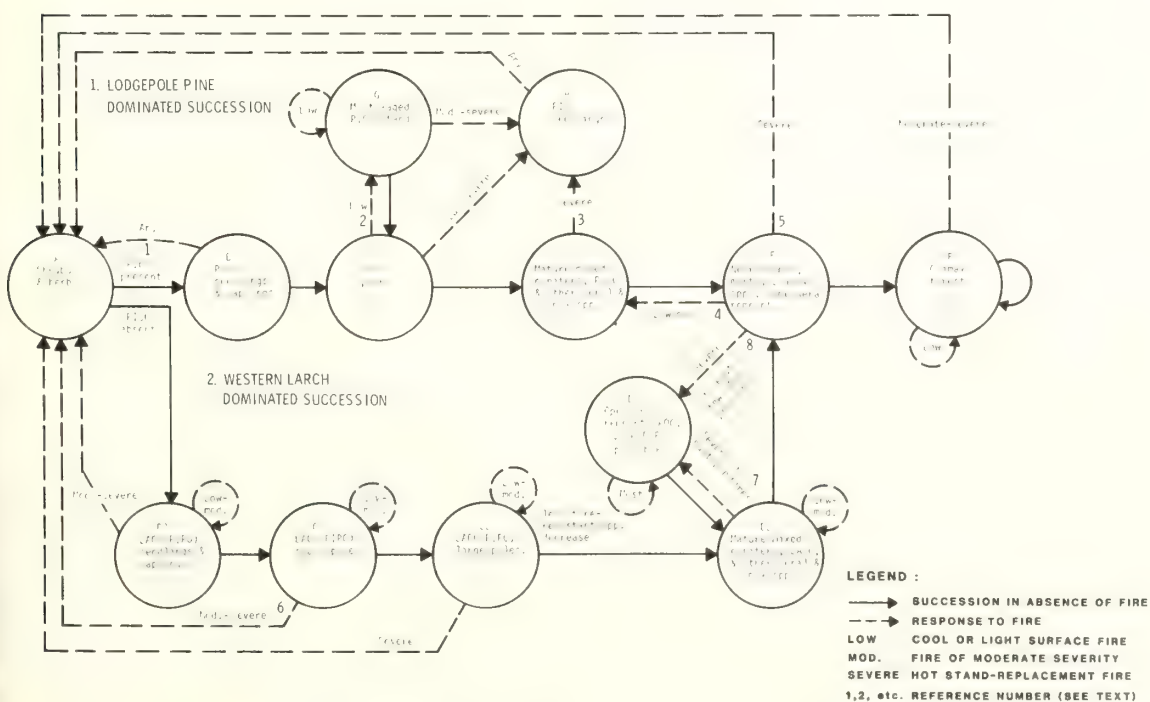


Figure 43—Hypothetical fire-related successional pathways for Fire Group Eleven habitat types.

Table 16—Recommended silvicultural procedures to obtain natural regeneration on the *Abies grandis*/*Clintonia uniflora* habitat type in the Swan Valley (after Antos and Shearer 1980)

Forest to be cut	Recommended procedure	Result
Mature forest on north or east slopes with larch	Clearcut or seed-tree ¹ cut leaving larch and Douglas-fir seed trees; site preparation by broadcast burning or scarification	Larch-dominated stand with some Douglas-fir and small amounts of other species mostly below the canopy
Mature forest on north slope with no larch	Seed-tree or shelterwood ¹ cut leaving Douglas-fir and mixture of other species, including white pine, grand fir, and spruce (leave spruce only if old ones are vigorous on site); site preparation by piling and burning (broadcast burning if thin-barked trees are considered)	Mixed forest of Douglas-fir with some grand fir and white pine (spruce)
Mature forest on south or west slope or any other site where seedling establishment might be difficult; larch present	Shelterwood ¹ leaving mostly larch and Douglas-fir; site preparation by broadcast burning or piling and burning	Larch-dominated stand with varying amounts of Douglas-fir depending in part on seed source ratios in shelterwood
Mature forest on south slope or any other site where establishment might be difficult; larch absent	Shelterwood cut leaving mostly Douglas-fir; site preparation by broadcast burning or by piling and burning	Douglas-fir stand with some grand fir
Forest with groups of healthy advanced regeneration of Douglas-fir, usually in groups from light burns on dry sites	Combination of group selection and shelterwood cut; site preparation by piling and burning; broadcast burning might be possible in parts of area	Stand with two or more age class groups of Douglas-fir with some larch and grand fir

¹Remove seed trees and shelterwood trees as soon as adequate regeneration is well established.

The use of fire for site preparation will usually result in increased spring and summer browse for big game in addition to successful regeneration of seral tree species. Frequent burns will maintain shrubfields on south slopes for game winter range.

Moisture conditions are usually high enough to prevent serious heat damage by low-severity wildfire, especially in old stands. Low-severity or smoldering surface fires may cause some heat damage to grand fir, white pine, western hemlock, western redcedar, subalpine fir, and spruce. Surface fires often scar the base of these species, creating favorable entry points for decay organisms. During drought, the large, often rotten forest floor fuels can dry out. Fires that start under low fuel moisture conditions can be severe and can result in death for almost the entire stand. Summertime fuel moisture conditions in young stands are not nearly as high as in older more dense stands. Consequently, the effects of fire are often more severe than they are in older stands.

Group Eleven sites are often found between streams and forest roads in western Montana. Consequently, roadside fuel reduction activities often are concentrated in these habitats. Such programs should take into account the need for retaining some large woody material both for maintenance of site quality and for woodpecker food supply. Also, snags and snag patches should be retained for their value as nest trees for cavity-nesting birds.

REFERENCES

- Alexander, M. E.; Hawksworth, F. G. Wildland fires and dwarf mistletoes: a literature review of ecology and prescribed burning. General Technical Report RM-14. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1975. 12 p.
- Alexander, Robert T.; Sheppard, Wayne D. Silvical characteristics of Engelmann spruce. General Technical Report RM-114. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1984. 38 p.
- Allen, A. W. Habitat suitability index models: southern red-backed vole (Western United States). FWS/OBS - 10.42. Denver, CO: U.S. Department of the Interior, Fish and Wildlife Service; 1983. 14 p.
- Amman, G. D. The role of mountain pine beetle in lodgepole pine ecosystems: impact on succession. In: Mattson, W. J., ed. Proceedings in life sciences: the role of arthropods in forest ecosystems. New York: Springer-Verlag; 1977: 3-15.
- Antos, J. A.; Habeck, J. R. Successional development in *Abies grandis* (Dougl.) Forbs forests in the Swan Valley, western Montana. Northwest Science. 55(1): 26-39; 1981.
- Antos, J. A.; Shearer, R. C. Vegetation development on disturbed grand fir sites, Swan Valley, northwestern Montana. Research Paper INT-251. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 26 p.
- Arno, Stephen F. Ecology of alpine larch (*Larix lyallii* Panl.) in the Pacific Northwest. Missoula, MT: University of Montana; 1970. 264 p. Ph.D. dissertation.
- Arno, Stephen F. The historical role of fire in the Bitterroot National Forest. Research Paper INT-187. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1976. 29 p.
- Arno, Stephen F. Forest regions of Montana. Research Paper INT-218. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 39 p.
- Arno, Stephen F. Forest fire history in the Northern Rockies. Journal of Forestry. 78(8): 460-465; 1980.

- Arno, Stephen F. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94; 1986.
- Arno, Stephen F.; Davis, D. H. Fire history of western redcedar/hemlock forests in northern Idaho. In: *Proceedings of the fire history workshop*; 1980 October 20-24; Tucson, AZ. General Technical Report RM-81. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1980: 21-26.
- Arno, Stephen F.; Gruell, George E. Fire history at the forest-grassland ecotone in southwestern Montana. *Journal of Range Management*. 36(3): 332-336; 1983.
- Arno, Stephen F.; Gruell, George E. Douglas-fir encroachment into mountain grasslands in southwestern Montana. *Journal of Range Management*. 39(3): 272-275; 1986.
- Arno, Stephen F.; Hammerly, Ramona P. Timberline: mountain and arctic forest frontiers. Seattle, WA: The Mountaineers; 1984. 304 p.
- Arno, S. F.; Hoff, R. J. Whitebark pine. In: *Silvics of forest trees of the United States*. Agriculture Handbook. Washington, DC: U.S. Department of Agriculture, Forest Service; [in press].
- Arno, S. F.; Petersen, T. D. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Research Paper INT-301. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 8 p.
- Arno, S. F.; Simmerman, D. G. Succession after cutting and fire treatments on forest habitat types in western Montana. In: *Site preparation and fuels management on steep terrain: Proceedings of a symposium*; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 113-117.
- Arno, S. F.; Simmerman, D. G.; Keane, R. E. Forest succession on four habitat types in western Montana. General Technical Report INT-177. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1985. 74 p.
- Beaufait, W. R.; Hardy, C. E.; Fischer, W. C. Broadcast burning in larch-fir clearcuts. Research Paper INT-175 (rev.). Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 53 p.
- Bendell, J. F. Effects of fire on birds and mammals. In: Kozlowski, T.; Ahlgren, C. E., eds. *Fire and ecosystems*. New York: Academic Press; 1974: 73-138.
- Bernard, S. R.; Brown, K. F. Distribution of mammals, reptiles, and amphibians by BLM physiographic regions and A. W. Kuchler's associations for the eleven western States. Technical Note 301. Denver, CO: U.S. Department of the Interior, Bureau of Land Management; 1977. 169 p.
- Black, H. C.; Tabor, R. D. Mammals in western coniferous forest ecosystems: an annotated bibliography. Bulletin 2. Seattle, WA: U.S. International Biological Program, Ecosystem Analysis Studies, Coniferous Forest Biome; 1977. 199 p.
- Boss, A.; Dunbar, M.; Gacey, J.; Hanna, P.; Roth, M.; Grossarth, O. D. Elk-timber relationships of west-central Idaho. Boise, ID: U.S. Department of Agriculture, Forest Service, Boise and Payette National Forests; U.S. Department of the Interior, Bureau of Land Management; 1983. 34 p.
- Bradley, A. F. Rhizome morphology, soil distribution, and the potential fire survival of eight woody understory species in western Montana. Missoula, MT: University of Montana; 1984. 184 p. M.A. thesis.
- Brown, James K. Handbook for inventorying downed woody material. General Technical Report INT-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1974. 24 p.
- Brown, James K. Fire cycles and community dynamics in lodgepole pine forests. In: Baumgartner, D. M., ed. *Management of lodgepole pine ecosystems: symposium proceedings*; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1975: 429-456.
- Brown, James K.; Marsden, Michael A.; Ryan, Kevin C.; Reinhardt, Elizabeth D. Predicting duff and woody fuel consumed by prescribed fire in the Northern Rocky Mountains. Research Paper INT-337. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1985. 23 p.
- Brown, James K.; See, Thomas E. Downed dead woody fuel and biomass in the Northern Rocky Mountains. General Technical Report INT-117. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 48 p.
- Clements, F. E. The life history of lodgepole pine burn forests. Forest Service Bulletin 79. Washington, DC: U.S. Department of Agriculture, Forest Service; 1910. 56 p.
- Cole, D. M. Feasibility of silvicultural practices for reducing losses to the mountain pine beetle in lodgepole pine forests. In: *Theory and practice of mountain pine beetle management in lodgepole pine forests: proceedings of the symposium*; 1978 April 25-27; Pullman, WA. Pullman, WA: Washington State University; 1978: 140-146.
- Cole, Walter E.; Amman, Gene D. Mountain pine beetle dynamics in lodgepole pine forests. Part I: Course of an infestation. General Technical Report INT-89. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 56 p.
- Crane, M. F.; Habeck, J. R.; Fischer, W. C. Early postfire revegetation in a western Montana Douglas-fir forest. Research Paper INT-319. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 32 p.
- Daubenmire, R. F. Vegetal zonation in the Rocky Mountains. *The Botanical Review*. 9(6): 325-393; 1943.
- Daubenmire, R.; Daubenmire, J. B. Forest vegetation of eastern Washington and north Idaho. Technical Bulletin 60. Pullman, WA: Washington Agricultural Experiment Station, Washington State University; 1968. 104 p.

- Davis, Kathleen M.; Clayton, Bruce D.; Fischer, William C. Fire ecology of Lolo National Forest habitat types. General Technical Report INT-79. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 77 p.
- Day, R. J. Stand structure succession and use of southern Alberta's Rocky Mountain forest. *Ecology*. 53(3): 472-477; 1972.
- DeByle, Norbert V. Clearcutting and fire in the larch/Douglas-fir forests of western Montana: a multifaceted research summary. General Technical Report INT-99. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 73 p.
- Despain, Don G. Vegetation of the Big Horn Mountains, Wyoming in relation to substrate and climate. *Ecological Monographs*. 43(3): 329-355; 1973.
- Despain, D. G.; Sellers, R. E. Natural fire in Yellowstone National Park. *Western Wildlands*. 4(1): 20-24; 1977.
- Eyre, F. H., ed. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters; 1980. 148 p.
- Fellin, D. G. A review of some interactions between harvesting, residue management, fire, and forest insects and diseases. In: Environmental consequences of timber harvesting in Rocky Mountain coniferous forests. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 335-414.
- Fischer, William C. Planning and evaluating prescribed fires—a standard procedure. General Technical Report INT-43. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1978. 19 p.
- Fischer, William C. Prescribed fire and bark beetle attack in ponderosa pine forests. *Fire Management Notes*. 41(2): 10-12; 1980.
- Fischer, William C. Photo guide for appraising downed woody fuels in Montana forests: interior ponderosa pine, ponderosa pine—western larch—Douglas-fir, western larch—Douglas-fir, and interior Douglas-fir cover types. General Technical Report INT-97. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981a. 133 p.
- Fischer, William C. Photo guide for appraising downed woody fuels in Montana forests: lodgepole pine and Engelmann spruce-subalpine fir cover types. General Technical Report INT-98. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981b. 143 p.
- Fischer, William C. Photo guide for appraising downed woody fuels in Montana forests: grand fir—larch—Douglas-fir, western hemlock, western hemlock—western redcedar, and western redcedar cover types. General Technical Report INT-96. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981c. 53 p.
- Fischer, William C. Wilderness fire management planning guide. General Technical Report INT-171. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1984. 56 p.
- Fischer, William C.; Clayton, B. D. Fire ecology of Montana forest habitat types east of the Continental Divide. General Technical Report INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 83 p.
- Flint, R. Fire resistance of Northern Rocky Mountain conifers. *Idaho Forester*. 7: 7-10, 40-43; 1925.
- Forcella, Frank; Weaver, T. Food production in the *Pinus albicaulis-Vaccinium scoparium* association. *Proceedings of the Montana Academy of Science*. 39: 73-80; 1980.
- Fowells, H. A. Silvics of forest trees of the United States. Agriculture Handbook 271. Washington, DC: U.S. Department of Agriculture, Forest Service; 1965. 762 p.
- Freedman, J. D. The historical relationship between fire and plant succession within the Swan Valley white-tailed deer winter range, western Montana. Missoula, MT: University of Montana; 1983. 137 p. Ph.D. dissertation.
- Freedman, J. D.; Habeck, J. R. Fire, logging and white-tailed deer, interrelationships in the Swan Valley, western Montana. In: Lotan, James E.; Brown, James K., compilers. Fire's effects on wildlife habitat—symposium proceedings; 1984 March 21; Missoula, MT. General Technical Report INT-186. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1985: 23-35.
- Gruell, George E.; Schmidt, Wyman C.; Arno, Stephen F.; Reich, William J. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana—implications for resource management. General Technical Report INT-130. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1982. 42 p.
- Habeck, James R. The composition of several climax forest communities in the McDonald area of Glacier National Park. *Proceedings of the Montana Academy of Science*. 23: 37-44; 1963.
- Habeck, James R. Forest succession in the Glacier Park cedar-hemlock forests. *Ecology*. 49(5): 872-880; 1968.
- Habeck, J. R. Fire ecology investigations in Glacier National Park. Missoula, MT: University of Montana, Department of Botany; 1970. 80 p.
- Habeck, J. R.; Mutch, R. W. Fire-dependent forests in the Northern Rocky Mountains. *Quaternary Research*. 3: 408-424; 1973.
- Habeck, J. R.; Weaver, T. W. A chemosystematic analysis of some hybrid spruce (*Picea*) populations in Montana. *Canadian Journal of Botany*. 47(10): 1565-1570; 1969.
- Halvorson, C. H. Small mammal populations. In: DeByle, N. V. Clearcutting and fire in the larch—Douglas-fir forests of western Montana: a multifaceted research summary. General Technical Report INT-99. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981: 41-46.

- Halvorson, C. H. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. *Ecology*. 63(2): 423-433; 1982.
- Harvey, A. E. The importance of residual organic debris in site preparation and amelioration for reforestation. In: Site preparation and fuels management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 75-85.
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Organic reserves: importance to ectomycorrhizae in forest soils of western Montana. *Forest Science*. 27(3): 442-445; 1981.
- Hendrickson, William H. Consideration of natural fire, variance in viewpoint. In: Role of fire in the Intermountain West. Missoula, MT: Intermountain Fire Research Council; 1970: 76-80.
- Hironaka, M.; Fosberg, M. A.; Winward, A. H. Sagebrush-grass habitat types of southern Idaho. *Bulletin* 35. Moscow, ID: University of Idaho, College of Forestry, Wildlife and Range Sciences; 1983. 44 p.
- Hobbs, N. T.; Spowart, R. A. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. *Journal of Wildlife Management*. 48(2): 551-560; 1984.
- Holdorf, H. Effects of site preparation and fuel management practices on soil productivity. In: Site preparation and fuels management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 63-65.
- Hutchins, H. E.; Lanner, R. M. The central role of Clark's nutcracker in the dispersal and establishment of white-bark pine. *Oecologia*. 55: 192-201; 1982.
- Kelsall, J. P.; Telfer, E. D.; Wright, T. D. The effects of fire on the ecology of the boreal forest, with particular reference to the Canadian north: a review and selected bibliography. Occasional Paper 32. Ottawa, ON: Fisheries and Environment Canada, Canadian Wildlife Service; 1977. 58 p.
- Kessell, Stephen R.; Fischer, William C. Predicting post-fire plant succession for fire management planning. General Technical Report INT-94. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 19 p.
- Kramer, Neal B. Mature forest seed banks on three habitat types in central Idaho. Moscow, ID: University of Idaho; 1984. 107 p. M.A. thesis.
- Kramp, B. A.; Patton, D. R.; Brady, W. W. The effects of fire on wildlife habitat and species. RUN WILD WILDLIFE/Habitat Relationships Technical Report. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region; 1983. 21 p.
- Kuglin, J. Beetles eat their way along Montana's backbone. *Missoulian*. 1980 January 17: 23.
- Little, Elbert L., Jr. Checklist of United States trees (native and naturalized). *Agriculture Handbook* 541. Washington, DC: U.S. Department of Agriculture, Forest Service; 1979. 375 p.
- Lotan, James E. Regeneration of lodgepole pine forests in the Northern Rocky Mountains. In: Baumgartner, E. M., ed. Management of lodgepole pine ecosystems: Symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1975: 516-535.
- Lotan, J. E.; Alexander, M. E.; Arno, S. F.; French, R. E.; Langdon, O. G.; Loomis, R. M.; Norum, R. A.; Rothermel, R. C.; Schmidt, W. C.; Van Wagtendonk, J. Effects of fire on flora: a state-of-knowledge review. General Technical Report WO-16. Washington, DC: U.S. Department of Agriculture, Forest Service; 1981. 71 p.
- Lotan, J. E.; Perry, D. A. Ecology and regeneration of lodgepole pine. *Agriculture Handbook* 606. Washington, DC: U.S. Department of Agriculture, Forest Service; 1983. 51 p.
- Lyon, L. Jack. Attrition of lodgepole pine snags of the Sleeping Child Burn, Montana. Research Note INT-219. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 4 p.
- Lyon, L. Jack; Stickney, Peter F. Early vegetal succession following large Northern Rocky Mountain wildfires. In: Proceedings, Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council Fire and Land Management Symposium; 1974 October 8-10; Missoula, MT. Tallahassee, FL: Tall Timbers Research Station; 1976: 355-375.
- Lyon, L. J. The Sleeping Child Burn—21 years of postfire change. Research Paper INT-330. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1984. 17 p.
- Lyon, L. J.; Crawford, H. S.; Czuttai, E.; Fredriksen, R. L.; Harlow, R. F.; Metz, L. J.; Pearson, H. A. Effects of fire on fauna. General Technical Report WO-6. Washington, DC: U.S. Department of Agriculture, Forest Service; 1978. 41 p.
- Maser, C.; Mate, B. R.; Franklin, J. F.; Dyrness, C. T. Natural history of Oregon coast mammals. General Technical Report PNW-133. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Forest and Range Experiment Station; 1981. 496 p.
- Mathews, E. E. The accretion of fuel in lodgepole pine forests of southwest Montana. Missoula, MT: University of Montana; 1980. 39 p. M.S. thesis.
- McClelland, B. R.; Frissell, S. S. Identifying forest snags useful for hole-nesting birds. *Journal of Forestry*. 73(7): 414-417; 1975.
- McClelland, B. R.; Frissell, S. S.; Fischer, W. C.; Halvorson, C. H. Habitat management for hole-nesting birds in western larch/Douglas-fir forests. *Journal of Forestry*. 77(8): 480-483; 1979.
- McGregor, M. D.; Cole, D. M., eds. Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. General Technical Report INT-174. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1985. 68 p.

- McLean, Alastair. Fire resistance of forest species as influenced by root systems. *Journal of Range Management*. 22(2): 120-122; 1969.
- Miller, M. Response of blue huckleberry to prescribed fires in a western Montana larch-fir forest. Research Paper INT-188. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 33 p.
- Minore, Don. Comparative autecological characteristics of northwestern tree species—a literature review. General Technical Report PNW-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1979. 72 p.
- Morgan, Penelope; Neuenschwander, L. F. Modeling shrub succession following clearcutting and broadcast burning. In: Lotan, James E.; Brown, James K., compilers. Fire's effect on wildlife habitat—symposium proceedings; 1984 March 21; Missoula, MT. General Technical Report INT-186. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1985: 83-90.
- Mueggler, W. F. Ecology of seral shrub communities in the cedar-hemlock zone of northern Idaho. *Ecological Monographs*. 35: 165-185; 1965.
- Muraro, S. J. The lodgepole pine fuel complex. Information Report BX-X-53. Victoria, BC: Department of Fisheries and Forestry, Canadian Forest Service, Forest Research Laboratory; 1971. 35 p.
- Nimir, M. B.; Payne, G. Effects of spring burning on a mountain range. *Journal of Range Management*. 31(4): 259-263; 1978.
- Nord, E. C. Autecology of bitterbrush in California. *Ecological Monographs*. 35: 307-334; 1965.
- Norum, Rodney A. Preliminary guidelines for prescribed burning under standing timber in western larch/Douglas-fir forests. Research Note INT-229. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 15 p.
- Noste, Nonan V. Influence of fire severity on response of evergreen ceanothus. In: Lotan, James E.; Brown, James K., compilers. Fire's effects on wildlife habitat—symposium proceedings; 1984 March 21; Missoula, MT. General Technical Report INT-186. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1985: 91-96.
- Perry, David A.; Lotan, James E. A model of fire selection for serotiny in lodgepole pine. *Evolution*. 33(3): 958-968; 1979.
- Pfister, R. D.; Daubenmire, R. Ecology of lodgepole pine, *Pinus contorta* Dougl. In: Baumgartner, D. M., ed. Management of lodgepole pine ecosystems: Symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1975: 27-46.
- Pfister, Robert D.; Kolvalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. Forest habitat types of Montana. General Technical Report INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 174 p.
- Ream, C. H. The effects of fire and other disturbances on small mammals and their predators: an annotated bibliography. General Technical Report INT-106. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 55 p.
- Ream, C. H.; Gruell, G. E. Influence of harvesting and residue treatments on small mammals and implications on forest management. In: Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: Proceedings of a symposium; 1979 September 11-13; Missoula, MT. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 455-467.
- Roberts, David W. Forest habitat types of the Bear's Paw Mountains and Little Rocky Mountains, Montana. Missoula, MT: University of Montana; 1980. 116 p. M.S. thesis.
- Roberts, David W.; Sibbernsen, John I. Forest and woodland habitat types of north central Montana. Volume 2: the Missouri River Breaks. Final Report, Contract No. YA-512-CT6-84. Billings, MT: U.S. Department of the Interior, Bureau of Land Management; 1979. 24 p.
- Roe, A. L.; Alexander, R.; Andrews, M. D. Engelmann spruce regeneration practices in the Rocky Mountains. Production Research Report 115. Washington, DC: U.S. Department of Agriculture, Forest Service; 1970. 32 p.
- Romme, William H. Fire frequency in subalpine forests of Yellowstone National Park. In: Proceedings of the fire history workshop; 1980 October 20-24; Tucson, AZ. General Technical Report RM-81. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1980: 27-30.
- Romme, W. H. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs*. 52(2): 199-221; 1982.
- Rowe, J. S. Concepts of fire effects on plant individuals and species. In: Wein, R. W.; MacLean, D. A., eds. The role of fire in northern circumpolar ecosystems. SCOPE 18 Series. Chichester, UK: John Wiley & Sons; 1983: 135-154.
- Schneegas, E. R.; Bumstead, R. S. Decline of western mule deer populations: probable cause and tentative solution. Presented at: 57th Annual Conference Western Associated State Game and Fish Commissioners; 1977 July 12; Tucson, AZ. 15 p.
- Schwennesen, D. Epidemics part of a revolution, Iverson says. *Missoulian*. 1979 October: 24.
- Shearer, R. C.; Schmidt, J. A. Reforesting a burned shrub-field and clearcut on a steep slope in a western larch forest of northwest Montana. In: Site preparation and fuel management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 159-165.
- Sneck (Davis), Kathleen M. The fire history of Coram Experimental Forest. Missoula, MT: University of Montana; 1977. 134 p. M.S. thesis.

- Society of American Foresters. Forestry terminology. 3d ed. Baltimore: Monumental Printing Co.; 1958. 97 p.
- Stark, N. Fire and nutrient cycling in a Douglas-fir/larch forest. *Ecology*. 58: 16-30; 1977.
- Stark, N.; Steele, R. W. Nutrient content of forest shrubs following burning. *American Journal of Botany*. 64(10): 1218-1224; 1977.
- Steele, R. W.; Beaufait, W. R. Spring and autumn broadcast burning of interior Douglas-fir slash. *Bulletin* 36. Missoula, MT: Montana Forest and Conservation Experiment Station; 1969. 12 p.
- Stevens, R. D.; Hall, R. C. Beetles and burned timber. Miscellaneous Paper 49. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1960. 2 p.
- Stickney, P. F. Vegetative recovery and development. In: DeByle, N. V. Clearcutting and fire in the larch/Douglas-fir forest of western Montana: a multifaceted research summary. General Technical Report INT-99. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981: 33-40.
- Stickney, P. F. Vegetation response to clearcutting and broadcast burning on north and south slopes at Newman Ridge. In: Site preparation and fuel management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 159-165.
- Tackle, D. Ecology and silviculture of lodgepole pine. In: Proceedings of the Society of American Foresters; 1964 September 27-October 1; Denver, CO. Washington, DC: Society of American Foresters; 1965: 112-115.
- Thomas, J. W., tech. ed. Wildlife habitats in managed forests in the Blue Mountains of Oregon and Washington. Agriculture Handbook 553. Washington, DC: U.S. Department of Agriculture, Forest Service; 1979. 512 p.
- Tiedemann, A. T.; Klock, G. O. Development of vegetation after fire, seeding, and fertilization on the Entiat Experimental Forest. In: Proceedings, Tall Timbers Fire Ecology Conference No. 15; 1974 October 16-17; Portland, OR. Tallahassee, FL: Tall Timbers Research Station; 1976: 171-192.
- U.S. Department of Agriculture, Forest Service. Species list: birds, mammals, fish, reptiles, and amphibians for the Forest Service including separate lists for Idaho, Montana, and North Dakota. Publication R1-78-002. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region; 1978. 82 p.
- U.S. Department of Agriculture, Soil Conservation Service. National handbook of plant names. Exhibit 430-VI. Washington, DC; 1981. 194 p.
- Verner, J.; Bass, A. S., tech. coords. California wildlife and their habitats: western Sierra Nevada. General Technical Report PSW-37. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1980. 439 p.
- Vogel, Richard J.; Ryder, Calvin. Effects of slash burning on conifer reproduction in Montana's Mission Range. *Northwest Science*. 42(3): 135-147; 1969.
- Volland, L. A.; Dell, J. D. Fire effects on Pacific Northwest forest and range vegetation. R-6 Rm 067. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region; 1981. 23 p.
- Wagener, W. W. Preliminary guidelines for estimating the survival of fire-damaged trees. Research Note 98. Berkeley, CA: U.S. Department of Agriculture, Forest Service, California Forest and Range Experiment Station; 1955. 9 p.
- Wagener, Willis W. Guidelines for estimating the survival of fire-damaged trees in California. Miscellaneous Paper 60. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1961. 11 p.
- Walter, H. Effects of fire on wildlife communities. In: Mooney, H. A.; Conrad, C. E., eds. Environmental consequences of fire and fuel management in Mediterranean ecosystems: Proceedings of the symposium; 1977 August 1-5; Palo Alto, CA. General Technical Report WO-3. Washington, DC: U.S. Department of Agriculture, Forest Service; 1977: 183-192.
- Weaver, Harold. Effects of prescribed burning in second growth ponderosa pine. *Journal of Forestry*. 55: 823-826; 1957.
- Weaver, Harold. Ecological changes in the ponderosa pine forest of the Warm Springs Indian Reservation in Oregon. *Journal of Forestry*. 57: 15-20; 1959.
- Weaver, Harold. Implications of the Klamath fires of September 1959. *Journal of Forestry*. 59: 569-572; 1961.
- Weaver, Harold. Fire and its relationship to ponderosa pine. In: Proceedings, Tall Timbers Fire Ecology Conference No. 7; 1967 November 9-10; Lake County, CA. Tallahassee, FL: Tall Timbers Research Station; 1967: 127-149.
- Wellner, C. A. Fire history in the Northern Rocky Mountains. In: Role of fire in the Intermountain West: Proceedings of a symposium; 1970 October 27-29; Missoula, MT. Missoula, MT: Intermountain Fire Research Council; 1970: 42-64.
- Williams, W.; Bailey, A. W.; McLean, A.; Tucker, R. The effects of fall grazing or burning bluebunch wheatgrass range on forage selection by deer and cattle in spring. *Canadian Journal of Animal Science*. 60(1): 113-122; 1980.
- Wright, H. A. Shrub response to fire. In: Wildland shrubs—their biology and utilization. General Technical Report INT-1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1972: 204-217.
- Wright, H. A. The effect of fire on vegetation in ponderosa pine forests: a state-of-the-art review. Science Publication T-9-199. College Station, TX: Texas Tech University, College of Agriculture; 1978. 21 p.
- Wright, H. A. The role and use of fire in the semidesert grass-shrub type. General Technical Report INT-85. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 24 p.

- Wright, H. A.; Bailey, A. W. Fire ecology and prescribed burning in the Great Plains—a research review. General Technical Report INT-77. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 60 p.
- Wright, H. A.; Bailey, A. W. Fire ecology, United States and southern Canada. New York: John Wiley & Sons; 1982. 501 p.
- Wright, H. A.; Neuenschwander, L. F.; Britton, C. M. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities: a state-of-the-art review. General Technical Report INT-58. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 48 p.
- Daubenmire, R. Forest vegetation of northern Idaho and adjacent Washington and its bearings on concepts of vegetation classification. *Ecological Monographs*. 22: 301-330; 1952.
- Daubenmire, R. Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. *Ecological Monographs*. 26: 131-154; 1956.
- Daubenmire, R. Structure and ecology of coniferous forests of the Northern Rocky Mountains. In: *Coniferous forests of the Northern Rocky Mountains*. Missoula, MT: Center for Natural Resources; 1968: 25-41.
- Davis, K. P.; Klehm, K. A. Controlled burning in the western white pine types. *Journal of Forestry*. 37(5): 399-407; 1939.
- DeByle, N. V. Soil fertility as affected by broadcast burning following clearcutting in Northern Rocky Mountain larch/fir forests. In: *Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council Fire and Land Management Symposium*; 1974 October 8-10; Missoula, MT. Tallahassee, FL: Tall Timbers Research Station; 1976: 447-464.
- Fiedler, C. E. Regeneration of clearcuts within four habitat types in western Montana. In: *Site preparation and fuel management on steep terrain: Proceedings of a symposium*; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 139-147.
- Fischer, G. M. Comparative germination of tree species on various kinds of surface-soil material in the western white pine type. *Ecology*. 16(4): 606-611; 1935.
- Forsythe, W. L. Size influence on the postfire composition of a Rocky Mountain forest. Missoula, MT: University of Montana; 1975. 173 p. Ph.D. dissertation.
- Gabriel, H. W., III. Wilderness ecology: the Danaher Creek drainage, Bob Marshall Wilderness, Montana. Missoula, MT: University of Montana; 1976. 224 p. Ph.D. dissertation.
- Graham, R. T.; Wellner, C. A.; Ward, R. Mixed conifers; western white pine, and western redcedar. In: *Burns, R. M., tech. compiler. Silvicultural systems for the major forest types of the United States. Agriculture Handbook 445*. Washington, DC: U.S. Department of Agriculture, Forest Service; 1983: 67-69.
- Haasis, F. W.; Trupp, A. C. Temperature relations of lodgepole pine seed germination. *Ecology*. 12: 728-774; 1931.
- Habeck, J. R. Fire ecology investigation in the Selway-Bitterroot Wilderness—historical considerations and current observations. Publication R172-991. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region; 1972. 119 p.
- Haig, I. T. Premature germination of forest tree seed during natural storage in duff. *Ecology*. 13: 311-312; 1932.
- Haig, I. T.; Davis, K. P.; Widman, R. H. Natural regeneration in the western white pine type. *Technical Bulletin 767*. Washington, DC: U.S. Department of Agriculture, Forest Service; 1941. 99 p.
- Hann, W. J. A taxonomy for classification of seral vegetation of selected habitat types in western Montana. Moscow, ID: University of Idaho; 1982. 235 p. Ph.D. dissertation.

OTHER REFERENCES

- Aller, A. R. The composition of the Lake McDonald Forest, Glacier National Park. *Ecology*. 41(1): 29-33; 1960.
- Amman, G. D.; McGregor, M. D.; Cahill, D. B.; Klein, W. H. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. General Technical Report INT-36. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 19 p.
- Antos, J.; McCune, B.; Bara, C. The effect of fire on an ungrazed western Montana grassland. *American Midland Naturalist*. 110(2): 354-364; 1983.
- Bates, C. G. Physiological requirements of Rocky Mountain trees. *Journal of Agricultural Research*. 24: 97-164; 1923.
- Baumgartner, D. M., ed. Management of lodgepole pine ecosystems: Proceedings of a symposium; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1975. 2 vol., 825 p.
- Biswell, H. H. Fire ecology in ponderosa pine grassland. In: *Proceedings, Tall Timbers Fire Ecology Conference No. 12*; 1972 June 8-9; Lubbock, TX. Tallahassee, FL: Tall Timbers Research Station; 1973: 69-96.
- Bloomberg, W. J. Fire and spruce. *Forestry Chronicle*. 26(2): 157-161; 1950.
- Boyd, R. J. Some case histories of natural regeneration in the western white pine type. Research Paper INT-63. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1969. 24 p.
- Boyd, R. J.; Deitschman, G. H. Site preparation aids natural regeneration in western larch-Engelmann spruce strip clearcutting. Research Paper INT-64. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1969. 10 p.
- Brown, A. A.; Davis, K. P. Forest fire control and use. New York: McGraw-Hill; 1973. 686 p.
- Critchfield, W. B. Geographic variation in *Pinus contorta*. Publication 3. New York: Columbia University, Maria Moors Cabot Foundation; 1957. 118 p.

- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Intensive fiber utilization and prescribed fire: effects on the microbial ecology of forests. General Technical Report INT-28. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1976. 46 p.
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. *Forest Science*. 24(2): 203-208; 1979.
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. *Forest Science*. 22: 393-398; 1976.
- Hodson, E. R.; Foster, J. H. Engelmann spruce in the Rocky Mountains. Circular 170. Washington, DC: U.S. Department of Agriculture, Forest Service; 1910. 23 p.
- Illingworth, K. Lodgepole pine provenance research and breeding in British Columbia. In: Baumgartner, D. M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1975: 47-67.
- Jurgensen, J.; Harvey, A.; Larsen, M. Effects of prescribed fire on soil nitrogen levels in a cutover Douglas-fir/western larch forest. Research Paper INT-275. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 6 p.
- Keen, F. P. Longevity of ponderosa pine. *Journal of Forestry*. 38: 597-598; 1940.
- Larsen, J. A. Some characteristics of seeds of coniferous trees from the Pacific Northwest. *National Nurseryman*. 30: 246-249; 1922.
- Larsen, J. A. Fires and forest succession in the Bitterroot Mountains of northern Idaho. *Ecology*. 10(1): 67-76; 1929.
- Larsen, J. A. Forest types of the Northern Rocky Mountains and their climatic controls. *Ecology*. 11(4): 631-672; 1930.
- Larsen, M. J.; Jurgensen, M. F.; Harvey, A. E. N₂ fixation associated with the wood decayed by some common fungi in western Montana. *Canadian Journal of Forest Research*. 8: 341-345; 1978.
- Leiberg, J. B. The Bitterroot Forest Reserve. In: 20th Annual Report. Part V: Forest Reserves. Washington, DC: U.S. Department of the Interior, Geological Survey; 1900a: 317-410.
- Leiberg, J. B. Cascade Range Forest Reserve, Oregon. In: Annual Report 21, 1899-1900. Part V: Forest Reserves. Washington, DC: U.S. Department of the Interior, Geological Survey; 1900b: 209-298.
- Lieu, P. J.; Kelsey, R. G.; Shafizadeh, F. Some chemical characteristics of green and dead lodgepole pine and western white pine. Research Note INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 8 p.
- Lotan, James E. Cone serotiny in *Pinus contorta*. Ann Arbor, MI: University of Michigan; 1970. 94 p. Ph.D. dissertation.
- Lotan, J. E. Cone serotiny-fire relationships in lodgepole pine. In: Proceedings, Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council Fire and Land Management Symposium; 1974 October 8-10; Missoula, MT. Tallahassee, FL: Tall Timbers Research Station; 1976: 267-278.
- Lunan, J. S.; Habeck, J. R. The effects of fire exclusion on ponderosa pine communities in Glacier National Park, Montana. *Canadian Journal of Forest Research*. 3: 574-579; 1973.
- Lynch, D. W. Effects of a wildfire on mortality and growth of young ponderosa pine trees. Research Note 66. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1959. 8 p.
- Lyon, L. J. Vegetal development on the Sleeping Child Burn in western Montana, 1961-1973. Research Paper INT-184. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1976. 24 p.
- MacKenzie, G. A. The fire ecology of the forest of Waterton Lakes National Park. Calgary, AB: University of Calgary; 1973. 199 p. M.S. thesis.
- Marshall, R. The life history of some western white pine stands on the Kaniksu National Forest. *Northwest Science*. 2(2): 48-53; 1928.
- Mason, D. T. The life history of lodgepole pine in the Rocky Mountains. *Agriculture Bulletin* 154. Washington, DC: U.S. Department of Agriculture, Forest Service; 1915. 135 p.
- McClelland, R. Riley. Wildfire influences on aesthetic values in Glacier National Park. *Western Wildlands*. 4(1): 23-30; 1977.
- McCune, B. Site, history, and forest dynamics in the Bitterroot Canyons Montana. Madison, WI: University of Wisconsin; 1982. 166 p. Ph.D. dissertation.
- McCune, Bruce. Fire frequency reduced two orders of magnitude in the Bitterroot Canyons. *Canadian Journal of Forest Research*. 13: 212-218; 1983.
- McCune, B.; Antos, J. A. Correlations between forest layers in the Swan Valley, Montana. *Ecology*. 62(5): 1196-1204; 1981.
- Miller, J. Effect of growing season on sprouting of blue huckleberry. Research Note INT-240. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1978. 8 p.
- Moir, W. H. Influence of ponderosa pine on herbaceous vegetation. *Ecology*. 47: 1045-1048; 1966.
- Morris, W. G.; Mowat, E. L. Some effects of thinning of a ponderosa pine thicket with fire. *Journal of Forestry*. 56: 203-209; 1958.
- Noste, N. V. Vegetation response to spring and fall burning for wildlife habitat improvement. In: Site preparation and fuel management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 125-132.
- Oliver, C. D.; Kenady, R. M. Proceedings of the biology and management of true fir in the Pacific Northwest symposium; 1981 February 24-26; Seattle, WA. Contribution Number 45. Seattle, WA: University of Washington, College of Forest Resources, Institute of Forest Resources; 1981. 344 p.

- Parker, A. J. Comparative structural/functional features in conifer forests of Yosemite and Glacier National Parks, USA. *American Midland Naturalist*. 197(1): 55-68; 1982.
- Pearson, G. A. Factors controlling the distribution of forest types. *Ecology*. 1: 139-150, 289-308; 1920.
- Phillips, T. A. The effects of fire on vegetation and wildlife on a lodgepole pine burn in Chamberlain Basin, Idaho. Progress Report. McCall, ID: U.S. Department of Agriculture, Forest Service; 1971. 9 p.
- Roe, A. L.; Amman, G. D. The mountain pine beetle in lodgepole pine forests. Research Paper INT-71. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1970. 23 p.
- Roeser, J. Transpiration capacity of coniferous seedlings and the problem of heat injury. *Journal of Forestry*. 30: 381-395; 1932.
- Ryan, K. C. Burning for site preparation on steep-slope helicopter-logged clearcuts in northwestern Montana. In: Site preparation and fuel management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 25-33.
- Schuler, J. H. The composition and distribution of Douglas-fir forest communities in the Pattee Canyon area, Missoula, Montana. Missoula, MT: University of Montana, Department of Botany; 1968. 84 p. Ph.D. dissertation.
- Shearer, R. C. Seedbed characteristics in western larch forest after prescribed burning. Research Paper INT-167. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1975. 26 p.
- Shearer, R. C. Establishment and growth of natural and planted conifers 10 years after clearcutting and burning in a Montana larch forest. In: Site preparation and fuel management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service; 1982: 149-157.
- Singer, F. J. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. *Journal of Wildlife Management*. 43(2): 437-444; 1979.
- Stahelin, R. Factors influencing the natural restocking of high altitude burns by coniferous trees in the Central Rocky Mountains. *Ecology*. 24: 19-30; 1943.
- Starker, T. J. Fire resistance in the forest. *Journal of Forestry*. 32: 462-467; 1934.
- Tackle, David. Lodgepole pine management in the Intermountain Region: a problem analysis. Miscellaneous Publication 2. Ogden, UT: U.S. Department of Agriculture, Forest Service; 1954. 53 p.
- Taylor, A. R. Lightning effects on the forest complex. In: Proceedings, Tall Timbers Fire Ecology Conference No. 9; 1969 April 10-11; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research Station; 1969: 127-150.
- Weaver, H. Fire—nature's thinning agent in ponderosa pine stands. *Journal of Forestry*. 45: 437-444; 1947.
- Weaver, H. A. Preliminary report on prescribed burning in virgin ponderosa pine. *Journal of Forestry*. 50: 662-667; 1952.
- Weaver, H. Fire as an enemy, friend, and tool in forest management. *Journal of Forestry*. 53: 499-504; 1955.
- Weaver, H. Effects of prescribed burning in ponderosa pine. *Journal of Forestry*. 55: 133-138; 1957.
- Weaver, H. Fire management problems in ponderosa pine. In: Proceedings, Tall Timbers Fire Ecology Conference No. 3; 1964 April 9-10; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research Station; 1964: 61-79.
- Weaver, H. Fire as a continuing ecological factor in perpetuation of ponderosa pine forests in the Western United States. *Advancing Frontiers of Plant Sciences*. New Delhi, India; 18: 137-154; 1967.
- Weaver, H. Effects of fire on temperate forests: Western United States. In: Kozlowski, T. T.; Ahlgren, C. E., eds. *Fire and ecosystems*. New York: Academic Press; 1974: 279-319.
- Weaver, T. Climates of vegetation types of the Northern Rocky Mountains and adjacent plains. *The American Midland Naturalist*. 103(2): 392-398; 1980.
- Whitford, H. N. The forests of the Flathead Valley, Montana. *Botanical Gazette*. 39: 99-122, 194-198, 276-296; 1905.
- Williamson, R. L. Natural regeneration of western hemlock. In: Proceedings of western hemlock management conference; 1976 May; Seattle, WA. Seattle, WA: University of Washington, College of Forest Resources; 1976: 166-169.
- Youngberg, C. T.; Dahms, W. J. Productivity indices for lodgepole pine on pumic soils. *Journal of Forestry*. 68: 90-94; 1970.

APPENDIX A: HABITAT TYPES OCCURRING WEST OF THE CONTINENTAL DIVIDE IN MONTANA

Abbreviations and scientific names are from Pfister and others' (1977) publication, "Forest Habitat Types of Montana." The "ADP codes" are the automatic data processing codes for National Forest System use.

Habitat types and phases			
ADP code	Abbreviation	Scientific name	Common name
PINUS PONDEROSA CLIMAX SERIES			
100			
130	PIPO/AGSP h.t.	<i>Pinus ponderosa</i> /Agropyron spicatum h.t.	ponderosa pine/bluebunch wheatgrass
140	PIPO/FEID h.t.	<i>Pinus ponderosa</i> /Festuca idahoensis h.t.	ponderosa pine/Idaho fescue
141	-FEID phase	-Festuca idahoensis phase	-Idaho fescue phase
142	-FESC phase	-Festuca scabrella phase	-rough fescue phase
160	PIPO/PUTR h.t.	<i>Pinus ponderosa</i> /Purshia tridentata h.t.	ponderosa pine/antelope bitterbrush
161	-AGSP phase	-Agropyron spicatum phase	-bluebunch wheatgrass phase
162	-FEID phase	-Festuca idahoensis phase	-Idaho fescue phase
170	PIPO/SYAL h.t.	<i>Pinus ponderosa</i> /Symphoricarpos albus h.t.	ponderosa pine/common snowberry
171	-SYAL phase	-Symphoricarpos albus phase	-common snowberry phase
PSEUDOTSUGA MENZIESII SERIES			
200			
210	PSME/AGSP h.t.	<i>Pseudotsuga menziesii</i> /Agropyron spicatum h.t.	Douglas-fir/bluebunch wheatgrass
220	PSME/FEID h.t.	<i>Pseudotsuga menziesii</i> /Festuca idahoensis h.t.	Douglas-fir/Idaho fescue
230	PSME/FESC h.t.	<i>Pseudotsuga menziesii</i> /Festuca scabrella h.t.	Douglas-fir/rough fescue
250	PSME/VACA h.t.	<i>Pseudotsuga menziesii</i> /Vaccinium caespitosum h.t.	Douglas-fir/dwarf huckleberry
260	PSME/PHMA h.t.	<i>Pseudotsuga menziesii</i> /Physocarpus malvaceus h.t.	Douglas-fir/mountain ninebark
261	-PHMA phase	-Physocarpus malvaceus phase	-mountain ninebark phase
262	-CARU phase	-Calamagrostis rubescens phase	-pinegrass phase
280	PSME/VAGL h.t.	<i>Pseudotsuga menziesii</i> /Vaccinium globulare h.t.	Douglas-fir/blue huckleberry
281	-VAGL phase	-Vaccinium globulare phase	-blue huckleberry phase
282	-ARUV phase	-Arctostaphylos uva-ursi phase	-kinnikinnick phase
283	-XETE phase	-Xerophyllum tenax phase	-beargrass phase
290	PSME/LIBO h.t.	<i>Pseudotsuga menziesii</i> /Linnaea borealis h.t.	Douglas-fir/twinflower
291	-SYAL phase	-Symphoricarpos albus phase	-common snowberry phase
292	-CARU phase	-Calamagrostis rubescens phase	-pinegrass phase
293	-VAGL phase	-Vaccinium globulare phase	-blue huckleberry phase
310	PSME/SYAL h.t.	<i>Pseudotsuga menziesii</i> /Symphoricarpos albus h.t.	Douglas-fir/common snowberry
311	-AFSP phase	-Agropyron spicatum phase	-bluebunch wheatgrass phase
312	-CARU phase	-Calamagrostis rubescens phase	-pinegrass phase
313	-SYAL phase	-Symphoricarpos albus phase	-common snowberry phase
320	PSME/CARU h.t.	<i>Pseudotsuga menziesii</i> /Calamagrostis rubescens h.t.	Douglas-fir/pinegrass
321	-AGSP phase	-Agropyron spicatum phase	-bluebunch wheatgrass phase
322	-ARUV phase	-Arctostaphylos uva-ursi phase	-kinnikinnick phase
323	-CARU phase	-Calamagrostis rubescens phase	-pinegrass phase
324	-PIPO phase	-Pinus ponderosa phase	-ponderosa pine phase
330	PSME/CAGE h.t.	<i>Pseudotsuga menziesii</i> /Carex geyeri h.t.	Douglas-fir/elk sedge
340	PSME/SPBE h.t.	<i>Pseudotsuga menziesii</i> /Spiraea betulifolia h.t.	Douglas-fir/white spirea
PICEA CLIMAX SERIES			
400			
410	PICEA/EQAR h.t.	<i>Picea/Equisetum arvense</i> h.t.	spruce/common horsetail
440	PICEA/GATR h.t.	<i>Picea/Galium triflorum</i> h.t.	spruce/sweetscented bedstraw
450	PICEA/VACA h.t.	<i>Picea/Vaccinium caespitosum</i> h.t.	spruce/dwarf huckleberry
470	PICEA/LIBO h.t.	<i>Picea/Linnaea borealis</i> h.t.	spruce/twinflower
480	PICEA/SMST h.t.	<i>Picea/Smilacina stellata</i> h.t.	spruce/starry false Solomon's seal
ABIES GRANDIS CLIMAX SERIES			
500			
510	ABGR/XETE h.t.	<i>Abies grandis</i> /Xerophyllum tenax h.t.	grand fir/common beargrass
520	ABGR/CLUN h.t.	<i>Abies grandis</i> /Clintonia uniflora h.t.	grand fir/queencup beadlily
521	-CLUN phase	-Clintonia uniflora phase	-queencup beadlily phase
522	-ARNU phase	-Aralia nudicaulis phase	-wild sarsaparilla phase
523	-XETE phase	-Xerophyllum tenax phase	-beargrass phase

(con.)

APPENDIX A (Con.)

			Habitat types and phases	
ADP code	Abbreviation	Scientific name	Common name	
501		THUJA PLICATA CLIMAX SERIES		
530	THPL/CLUN h.t.	<i>Thuja plicata</i> / <i>Clintonia uniflora</i> h.t.	western redcedar/queencup beadlily	
531	-CLUN phase	- <i>Clintonia uniflora</i> phase	-queencup beadlily phase	
532	-ARNU phase	- <i>Aralia nudicaulis</i> phase	-wild sarsaparilla phase	
533	-MEFE phase	- <i>Menziesia ferruginea</i> phase	-menziesia phase	
550	THPL/OPHO h.t.	<i>Thuja plicata</i> / <i>Oplopanax horridum</i> h.t.	western redcedar/devil's club	
590	ABGR/LIBO h.t.	<i>Abies grandis</i> / <i>Linnaea borealis</i> h.t.	grand fir/twinflower	
591	-LIBO phase	- <i>Linnaea borealis</i> phase	-twinflower phase	
592	-XETE phase	- <i>Xerophyllum tenax</i> phase	-beargrass phase	
502		TSUGA HETEROPHYLLA CLIMAX SERIES		
570	TSHE/CLUN h.t.	<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i>	western hemlock/queencup beadlily	
571	-CLUN phase	- <i>Clintonia uniflora</i> phase	-queencup beadlily phase	
572	-ARNU phase	- <i>Aralia nudicaulis</i> phase	-wild sarsaparilla phase	
600		ABIES LASIOCARPA CLIMAX SERIES		
700		Lower subalpine h.t.'s		
610	ABLA/OPHO h.t.	<i>Abies lasiocarpa</i> / <i>Oplopanax horridum</i> h.t.	subalpine fir/devil's club	
620	ABLA/CLUN h.t.	<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> h.t.	subalpine fir/queencup beadlily	
621	-CLUN phase	- <i>Clintonia uniflora</i> phase	-queencup beadlily phase	
622	-ARNU phase	- <i>Aralia nudicaulis</i> phase	-wild sarsaparilla phase	
623	-VACA phase	- <i>Vaccinium caespitosum</i> phase	-dwarf huckleberry phase	
624	-XETE phase	- <i>Xerophyllum tenax</i> phase	-beargrass phase	
625	-MEFE phase	- <i>Menziesia ferruginea</i> phase	-menziesia phase	
630	ABLA/GATR h.t.	<i>Abies lasiocarpa</i> / <i>Galium triflorum</i> h.t.	subalpine fir/sweetscented bedstraw	
640	ABLA/VACA h.t.	<i>Abies lasiocarpa</i> / <i>Vaccinium caespitosum</i> h.t.	subalpine fir/dwarf huckleberry	
650	ABLA/CACA h.t.	<i>Abies lasiocarpa</i> / <i>Calamagrostis canadensis</i> h.t.	subalpine fir/bluejoint	
651	-CACA phase	- <i>Calamagrostis canadensis</i> phase	-bluejoint phase	
653	-GATR phase	- <i>Galium triflorum</i> phase	-sweetscented bedstraw phase	
654	-VACA phase	- <i>Vaccinium caespitosum</i> phase	-dwarf huckleberry phase	
660	ABLA/LIBO h.t.	<i>Abies lasiocarpa</i> / <i>Linnaea borealis</i> h.t.	subalpine fir/twinflower	
661	-LIBO phase	- <i>Linnaea borealis</i> phase	-twinflower phase	
662	-XETE phase	- <i>Xerophyllum tenax</i> phase	-beargrass phase	
663	-VASC phase	- <i>Vaccinium scoparium</i> phase	-grouse whortleberry phase	
670	ABLA/MEFE h.t.	<i>Abies lasiocarpa</i> / <i>Menziesia ferruginea</i> h.t.	subalpine fir/menziesia	
680	TSME/MEFE h.t.	<i>Tsuga mertensiana</i> / <i>Menziesia ferruginea</i> h.t.	mountain hemlock/menziesia	
690	ABLAXETE h.t.	<i>Abies lasiocarpa</i> / <i>Xerophyllum tenax</i> h.t.	subalpine fir/beargrass	
691	-VAGL phase	- <i>Vaccinium globulare</i> phase	-blue huckleberry phase	
692	-VASC phase	- <i>Vaccinium scoparium</i> phase	-grouse whortleberry phase	
710	TSME/XETE h.t.	<i>Tsuga mertensiana</i> / <i>Xerophyllum tenax</i> h.t.	mountain hemlock/beargrass	
720	ABLA/VAGL h.t.	<i>Abies lasiocarpa</i> / <i>Vaccinium globulare</i> h.t.	subalpine fir/blue huckleberry	
730	ABLA/VASC h.t.	<i>Abies lasiocarpa</i> / <i>Vaccinium scoparium</i> h.t.	subalpine fir/grouse whortleberry	
731	-VASC h.t.	- <i>Vaccinium scoparium</i> phase	-grouse whortleberry phase	
800		Upper subalpine h.t.'s		
820	ABLA-PIAL/VASC h.t.	<i>Abies lasiocarpa</i> - <i>Pinus albicaulis</i> / <i>Vaccinium scoparium</i> h.t.	subalpine fir-whitebark pine/grouse whortleberry	
830	ABLA/LUHI h.t.	<i>Abies lasiocarpa</i> / <i>Luzula hitchcockii</i> h.t.	subalpine fir/smooth woodrush	
831	-VASC phase	- <i>Vaccinium scoparium</i> phase	-grouse whortleberry phase	
832	-MEFE phase	- <i>Menziesia ferruginea</i> phase	-menziesia phase	
840	TSME/LUHI h.t.	<i>Tsuga mertensiana</i> / <i>Luzula hitchcockii</i> h.t.	mountain hemlock/smooth woodrush	
841	-VASC phase	- <i>Vaccinium scoparium</i> phase	-grouse whortleberry phase	
842	-MEFE phase	- <i>Menziesia ferruginea</i> phase	-menziesia phase	
890		Timberline h.t.'s		
850	PIAL-ABLA h.t.'s	<i>Pinus albicaulis</i> - <i>Abies lasiocarpa</i> h.t.'s	whitebark pine-subalpine fir	
860	LALY-ABLA h.t.'s	<i>Larix lyallii</i> - <i>Abies lasiocarpa</i> h.t.'s	subalpine larch-subalpine fir	
870	PIAL h.t.'s	<i>Pinus albicaulis</i> h.t.'s	whitebark pine	

APPENDIX B: DYNAMIC STATUS OF TREE SPECIES

Distribution of tree species in western Montana habitat types showing their dynamic status as interpreted from sample stand data (after Pfister and others 1977).

Fire Group	Habitat type-phase	Tree species														
		JUSC	PIPO	PSME	PICO	LAOC	PICEA	ABGR	PIMO	THPL	TSHE	ABLA	TSME	PIAL	LALY	BEPA
2	PIPO/AGSP	(F)	C	a	-	-	-	-	-	-	-	-	-	-	-	-
	PIPO/FEID-FEID	a	C	a	-	-	-	-	-	-	-	-	-	-	-	-
	PIPO/FEID-FESC	a	C	a	-	-	-	-	-	-	-	-	-	-	-	-
	PIPO/FEID-AGSP	a	C	a	-	-	-	-	-	-	-	-	-	-	-	-
	PIPO/PUTR-FEID	(c)	C	a	-	-	-	-	-	-	-	-	-	-	-	-
	PIPO/SYAL-SYAL	a	C	a	-	-	-	-	-	-	-	-	-	-	-	-
4	PSME/AGSP	(c)	C	C	-	-	-	-	-	-	-	-	-	-	-	-
	PSME/FESC	a	C	C	-	-	-	-	-	-	-	-	-	-	-	-
	PSME/PHMA-CARU	-	S	C	a	a	-	-	-	-	-	-	-	-	-	-
	PSME/SYAL-AGSP	-	S	C	-	-	-	-	-	-	-	-	-	-	-	-
	PSME/CARU-AGSP	-	S	C	-	-	-	-	-	-	-	-	-	-	-	-
	PSME/CARU-PIPO	-	S	C	-	-	-	-	-	-	-	-	-	-	-	-
	PSME/SPBE	-	(S)	C	a	a	-	-	-	-	-	-	-	-	-	-
5	PSME/FEID	a	a	C	-	-	-	-	-	-	-	-	-	-	-	-
	PSME/CAGE	-	(s)	C	a	a	-	-	-	-	-	-	-	-	-	-
6	PSME/VACA	-	(S)	C	S	(S)	a	-	-	-	-	a	-	-	-	-
	PSME/PHMA-PHMA	-	(s)	C	(s)	(s)	-	a	-	-	-	-	-	-	-	-
	PSME/VAGL-VAGL	-	(s)	C	S	(s)	a	-	-	-	-	a	-	a	-	-
	PSME/VAGL-ARUV	-	S	C	(s)	(s)	-	a	-	-	-	-	-	-	-	-
	PSME/VAGL-XETE	-	(s)	C	S	(S)	-	a	-	-	-	a	-	a	-	-
	PSME/LIBO-SYAL	-	(s)	C	(s)	(S)	-	-	-	-	-	-	-	-	-	-
	PSME/LIBO-CARU	-	(s)	C	(S)	(S)	-	-	-	-	-	a	-	-	-	-
	PSME/LIBO-VAGL	-	(s)	C	S	(s)	a	a	-	-	-	a	-	-	-	-
	PSME/SYAL-CARU	-	(s)	C	(s)	a	a	-	-	-	-	-	-	-	-	-
	PSME/SYAL-SYAL	-	(s)	C	(s)	-	-	-	-	-	-	-	-	a	-	-
	PSME/CARU-ARUV	-	S	C	s	s	-	-	-	-	-	-	-	-	-	-
PSME/CARU-CARU	-	a	C	(S)	(s)	-	-	-	-	-	a	-	a	-	-	
7	PSME/VACA	-	(S)	C	S	(S)	a	-	-	-	-	a	-	-	-	-
	PICEA/VACA	-	(s)	S	S	S	C	-	-	-	-	a	-	-	-	-
	PICEA/LIBO	-	a	S	S	-	C	-	-	-	-	a	-	a	-	-
	ABLA/VACA	-	-	(s)	S	a	(c)	-	-	-	-	c	-	a	-	-
	ABLA/CACA-VACA	-	-	a	S	-	s	-	-	-	-	C	-	a	-	-
	ABLA/LIBO-VASC	-	-	s	S	a	s	-	-	-	-	C	-	a	-	-
	ABLA/XETE-VASC	-	-	(s)	S	-	s	-	-	-	-	C	a	(s)	-	-
	ABLA/VAGL	-	-	S	S	-	(s)	-	-	-	-	C	-	s	-	-
	ABLA/VASC-VASC	-	-	a	S	-	(s)	-	-	-	-	C	-	s	-	-
	PICO/LIBO															
PICO/VASC																
8	PICEA/SMST	-	(s)	S	S	-	C	-	-	-	-	a	-	a	-	-
	ABLA/XETE-VAGL	-	(s)	S	S	(s)	s	a	(s)	-	-	C	a	(s)	-	-
	TSME/MEFE	-	-	(s)	s	s	s	-	(s)	-	-	C	C	(s)	-	-

(con.)

APPENDIX B (Con.)

Fire Group	Habitat type-phase	Tree species														
		JUSC	PIPO	PSME	PICO	LAOC	PICEA	ABGR	PIMO	THPL	TSHE	ABLA	TSME	PIAL	LALY	BEPA
9	PICEA/EQAR	-	-	a	a	-	C	-	-	-	-	a	-	-	-	(s)
	PICEA/CLUN-VACA	-	(s)	S	S	S	C	-	a	-	-	a	-	-	-	-
	PICEA/CLUN-CLUN	-	(s)	S	(S)	S	C	-	a	-	-	a	-	-	-	(S)
	PICEA/GATR	-	(s)	S	S	-	C	-	-	-	-	a	-	a	-	-
	ABLA/OPHO	-	-	s	-	s	S	-	s	-	a	C	-	-	-	-
	ABLA/CLUN-CLUN	-	(s)	S	(S)	S	S	(s)	(s)	a	a	C	-	-	-	a
	ABLA/CLUN-ARNU	-	a	s	(s)	S	S	(s)	(s)	-	a	C	-	-	-	(S)
	ABLA/CLUN-VACA	-	(s)	S	S	s	s	a	a	-	-	C	-	a	-	-
	ABLA/CLUN-XETE	-	-	S	S	S	S	a	(s)	-	a	C	(c)	a	-	-
	ABLA/CLUN-MEFE	-	-	S	s	s	S	(C)	(s)	a	a	C	(c)	a	-	-
	ABLA/GATR	-	a	S	S	(s)	S	-	-	-	-	C	-	-	-	-
	ABLA/CACA-CACA	-	-	-	S	-	S	-	-	-	-	C	-	(s)	-	-
	ABLA/CACA-GATR	-	-	-	s	-	S	-	-	-	-	C	-	-	-	-
	ABLA/LIBO-LIBO	-	(s)	S	S	(S)	S	a	-	-	-	C	-	a	-	-
	ABLA/LIBO-XETE	-	a	S	S	S	s	a	(s)	-	-	C	-	-	-	-
	ABLA/MEFE	-	-	(S)	S	(s)	S	a	a	-	-	C	a	(s)	-	-
	TSME/MEFE	-	-	(s)	s	s	s	-	(s)	-	-	C	C	(s)	-	-
	ABLA/ALSI	-	-	(S)	S	-	S	-	-	-	-	C	-	(s)	-	-
10	ABLA-PIAL/VASC	-	-	-	(S)	-	S	-	-	-	-	C	-	S	-	-
	ABLA/LUHI-VASC	-	-	-	(s)	-	S	-	-	-	-	C	a	S	-	-
	ABLA/LUHI-MEFE	-	-	-	a	-	S	-	-	-	-	C	-	s	(C)	-
	TSME/LUHI-VASC	-	-	-	(s)	-	s	-	-	-	-	C	C	s	-	-
	TSME/LUHI-MEFE	-	-	-	a	-	s	-	-	-	-	(C)	C	a	-	-
	PIAL-ABLA h.t.'s	-	-	-	-	-	(C)	-	-	-	-	(C)	-	(C)	-	-
	LALY-ABLA h.t.'s	-	-	-	-	-	(c)	-	-	-	-	(C)	-	(C)	(C)	-
	PIAL h.t.'s	-	-	a	-	-	a	-	-	-	-	a	-	C	-	-
11	ABGR/XETE	-	s	S	S	S	a	C	a	a	-	a	-	-	-	-
	ABGR/CLUN-CLUN	-	(s)	S	(s)	(s)	(S)	C	(s)	a	-	(C)	-	-	-	-
	ABGR/CLUN-ARNU	-	a	S	a	S	S	C	(s)	a	a	a	-	-	-	s
	ABGR/CLUN-XETE	-	a	S	s	S	(S)	C	s	a	a	c	-	-	-	a
	ABGR/LIBO-LIBO	-	(s)	S	s	S	a	C	-	-	-	a	-	-	-	a
	ABGR/LIBO-XETE	-	(s)	S	s	s	a	C	-	-	-	-	-	-	-	-
	THPL/CLUN-CLUN	-	a	S	(s)	S	S	(c)	(s)	C	a	(c)	-	-	-	(s)
	THPL/CLUN-ARNU	-	-	S	a	S	(S)	(c)	(s)	C	(c)	(s)	-	-	-	(s)
	THPL/CLUN-MEFE	-	-	S	S	S	S	a	(s)	C	-	c	-	-	-	-
	THPL/OPHO	-	-	s	-	a	s	(s)	a	(C)	(C)	(c)	-	-	-	(s)
	TSHE/CLUN-ARNU	-	a	(s)	a	S	(S)	(c)	-	c	C	(c)	-	-	-	(s)
0	SCREE	-	(C)	C	a	-	(c)	-	-	-	-	(c)	-	(c)	-	-

C = major climax; S = major seral; a = accidental; c = minor climax; s = minor seral; () = in certain areas of the type.

APPENDIX C: HABITAT TYPE FIRE GROUPS FOR MONTANA FORESTS

Fire Group 0 - Miscellaneous special habitats:

- Scree;
- Forested rock;
- Meadow; Grassy bald; Alder glade; Aspen grove

Fire Group 1 - Dry limber pine habitat types:

- Pinus flexilis*/*Agropyron spicatum* (PIFL/AGSP; limber pine/bluebunch wheatgrass)
- Pinus flexilis*/*Festuca idahoensis* h.t.-*Festuca idahoensis* phase (PIFL/FEID-FEID; limber pine/Idaho fescue-rough fescue phase)
- Pinus flexilis*/*Festuca idahoensis* h.t.-*Festuca scabrella* phase (PIFL/FEID-FESC; limber pine/Idaho fescue-rough fescue phase)
- Pinus flexilis*/*Juniperus communis* h.t. (PIFL/JUCO; limber pine/common juniper)

Fire Group 2 - Warm, dry ponderosa pine habitat types:

- Pinus ponderosa*/*Andropogon* spp. h.t. (PIPO/AND; ponderosa pine/bluestem)
- Pinus ponderosa*/*Agropyron spicatum* h.t. (PIPO/AGSP; ponderosa pine/bluebunch wheatgrass)
- Pinus ponderosa*/*Festuca idahoensis*-*Festuca idahoensis* phase (PIPO/FEID-FEID; ponderosa pine/Idaho fescue-Idaho fescue phase)
- Pinus ponderosa*/*Festuca idahoensis* h.t.-*Festuca scabrella* phase (PIPO/FEID-FESC; ponderosa pine/Idaho fescue-rough fescue phase)
- Pinus ponderosa*/*Purshia tridentata* h.t.-*Agropyron spicatum* phase (PIPO/PUTR-AGSP; ponderosa pine/antelope bitterbrush-bluebunch wheatgrass phase)
- Pinus ponderosa*/*Purshia tridentata* h.t.-*Festuca idahoensis* phase (PIPO/PUTR-FEID; ponderosa pine/antelope bitterbrush-Idaho fescue phase)
- Pinus ponderosa*/*Symphoricarpos albus* h.t.-*Symphoricarpos albus* phase (PIPO/SYAL-SYAL; ponderosa pine/common snowberry-common snowberry phase)
- Pinus ponderosa*/*Symphoricarpos occidentalis* h.t. (PIPO/SYOC; ponderosa pine/western snowberry)
- Pinus ponderosa*/*Arctostaphylos uva-ursi* h.t. (PIPO/ARUV; ponderosa pine/kinnikinnick)
- Pinus ponderosa*/*Juniperus horizontalis* h.t. (PIPO/JUHO; ponderosa pine/creeping juniper)
- Pinus ponderosa*/*Juniperus scopulorum* h.t. (PIPO/JUSC; ponderosa pine/Rocky Mountain juniper)

Fire Group 3 - Warm, moist ponderosa pine habitat types:

- Pinus ponderosa*/*Symphoricarpos albus* h.t.-*Berberis repens* phase (PIPO/SYAL-BERE; ponderosa pine/common snowberry-hollygrape phase)
- Pinus ponderosa*/*Berberis repens* h.t. (PIPO/BERE; ponderosa pine/hollygrape)
- Pinus ponderosa*/*Amelanchier alnifolia* h.t. (PIPO/AMAL; ponderosa pine/western serviceberry)
- Pinus ponderosa*/*Prunus virginiana* h.t.-*Prunus virginiana* phase (PIPO/PRVI-PRVI; ponderosa pine/chokecherry-chokecherry phase)
- Pinus ponderosa*/*Prunus virginiana* h.t.-*Shepherdia canadensis* phase (PIPO/PRVI-SHCA; ponderosa pine/chokecherry-russet buffalo-berry phase)

Fire Group 4 - Warm, dry Douglas-fir habitat types:

- Pseudotsuga menziesii*/*Agropyron spicatum* h.t. (PSME/AGSP; Douglas-fir/bluebunch wheatgrass)
- Pseudotsuga menziesii*/*Festuca scabrella* h.t. (PSME/FESC; Douglas-fir/rough fescue)
- Pseudotsuga menziesii*/*Physocarpus malvaceus* h.t.-*Calamagrostis rubescens* phase (PSME/PHMA-CARU; Douglas-fir/mountain ninebark-pinegrass phase)
- Pseudotsuga menziesii*/*Symphoricarpos albus* h.t.-*Agropyron spicatum* phase (PSME/SYAL-AGSP; Douglas-fir/common snowberry-bluebunch wheatgrass phase)
- Pseudotsuga menziesii*/*Symphoricarpos occidentalis* h.t.-*Chrysopsis villosa* phase (PSME/SYOC-CHVI; Douglas-fir/western snowberry-hairy goldenaster phase)
- Pseudotsuga menziesii*/*Symphoricarpos occidentalis* h.t.-*Shepherdia canadensis* phase (PSME/SYOC-SHCA; Douglas-fir/western snowberry-russet buffaloberry phase)
- Pseudotsuga menziesii*/*Calamagrostis rubescens* h.t.-*Agropyron spicatum* phase (PSME/CARU-AGSP; Douglas-fir/pinegrass-bluebunch wheatgrass phase)
- Pseudotsuga menziesii*/*Calamagrostis rubescens* h.t.-*Pinus ponderosa* phase (PSME/CARU-PIPO; Douglas-fir/pinegrass-ponderosa pine phase)
- Pseudotsuga menziesii*/*Spiraea betulifolia* h.t. (PSME/SPBE; Douglas-fir/white spirea)
- Pseudotsuga menziesii*/*Arctostaphylos uva-ursi* h.t. (PSME/ARUV; Douglas-fir/kinnikinnick)
- Pseudotsuga menziesii*/*Berberis repens* h.t.-*Arctostaphylos uva-ursi* phase (PSME/BERE-ARUV; Douglas-fir/hollygrape-kinnikinnick phase)
- Pseudotsuga menziesii*/*Berberis repens* h.t.-*Berberis repens* phase (PSME/BERE-BERE; Douglas-fir/hollygrape-hollygrape phase)
- Pseudotsuga menziesii*/*Juniperus scopulorum* h.t. (PSME/JUSC; Douglas-fir/Rocky Mountain juniper)
- Pseudotsuga menziesii*/*Muhlenbergia cuspidata* h.t. (PSME/MUCU; Douglas-fir/plains muhly)

(con.)

APPENDIX C (Con.)

Fire Group 5 - Cool, dry Douglas-fir habitat types:

- Pseudotsuga menziesii/Calamagrostis rubescens* h.t.-*Agropyron spicatum* phase (PSME/CARU-AGSP; Douglas-fir/pinegrass-bluebunch wheatgrass phase)
- Pseudotsuga menziesii/Festuca idahoensis* h.t. (PSME/FEID; Douglas-fir/Idaho fescue)
- Pseudotsuga menziesii/Carex geyeri* h.t. (PSME/CAGE; Douglas-fir/elk sedge)
- Pseudotsuga menziesii/Arnica cordifolia* h.t. (PSME/ARCO; Douglas-fir/heartleaf arnica)
- Pseudotsuga menziesii/Symphoricarpos oreophilus* h.t. (PSME/SYOR; Douglas-fir/mountain snowberry)
- Picea/Senecio streptanthifolius* h.t.-*Pseudotsuga menziesii* phase (PICEA/SEST-PSME; spruce/cleftleaf groundsel-Douglas-fir phase)

Fire Group 6 - Moist Douglas-fir habitat types:

- Pseudotsuga menziesii/Physocarpus malvaceus* h.t.-*Physocarpus malvaceus* phase (PSME/PHMA-PHMA; Douglas-fir/mountain ninebark-mountain ninebark phase)
- Pseudotsuga menziesii/Viola canadensis* h.t. (PSME/VICA; Douglas-fir/Canada violet)
- Pseudotsuga menziesii/Vaccinium globulare* h.t.-*Vaccinium globulare* phase (PSME/VAGL-VAGL; Douglas-fir/blue huckleberry-blue huckleberry phase)
- Pseudotsuga menziesii/Vaccinium globulare* h.t.-*Arctostaphylos uva-ursi* phase (PSME/VAGL-ARUV; Douglas-fir/blue huckleberry-kinnikinnick phase)
- Pseudotsuga menziesii/Vaccinium globulare* h.t.-*Xerophyllum tenax* phase (PSME/VAGL-XETE; Douglas-fir/blue huckleberry-beargrass phase)
- Pseudotsuga menziesii/Linnaea borealis* h.t.-*Symphoricarpos albus* phase (PSME/LIBO-ARUV; Douglas-fir/twinflower-common snowberry phase)
- Pseudotsuga menziesii/Linnaea borealis* h.t.-*Arctostaphylos uva-ursi* phase (PSME/LIBO-ARUV; Douglas-fir/twinflower-kinnikinnick phase)
- Pseudotsuga menziesii/Linnaea borealis* h.t.-*Vaccinium globulare* phase (PSME/LIBO-VAGL; Douglas-fir/twinflower-blue huckleberry phase)
- Pseudotsuga menziesii/Symphoricarpos albus* h.t.-*Calamagrostis rubescens* phase (PSME/SYAL-CARU; Douglas-fir/common snowberry-pinegrass phase)
- Pseudotsuga menziesii/Symphoricarpos albus* h.t.-*Symphoricarpos albus* phase (PSME/SYAL-SYAL; Douglas-fir/common snowberry-common snowberry phase)
- Pseudotsuga menziesii/Amelanchier alnifolia* h.t. (PSME/AMAL; Douglas-fir/western serviceberry)
- Pseudotsuga menziesii/Calamagrostis rubescens* h.t.-*Arctostaphylos uva-ursi* phase (PSME/CARU-ARUV; Douglas-fir/pinegrass-kinnikinnick phase)
- Pseudotsuga menziesii/Calamagrostis rubescens* h.t.-*Calamagrostis rubescens* phase (PSME/CARU-CARU; Douglas-fir/pinegrass-pinegrass phase)
- Pseudotsuga menziesii/Vaccinium caespitosum* h.t. (PSME/VACA; Douglas-fir/dwarf huckleberry)
- Pseudotsuga menziesii/Juniperus communis* h.t. (PSME/JUCO; Douglas-fir/common juniper)

Fire Group 7 - Cool habitat types usually dominated by lodgepole pine:

- Pseudotsuga menziesii/Juniperus communis* h.t. (PSME/JUCO; Douglas-fir/common juniper)
- Pseudotsuga menziesii/Vaccinium caespitosum* h.t. (PSME/VACA; Douglas-fir/dwarf huckleberry)
- Pseudotsuga menziesii/Cornus canadensis* h.t.-*Linnaea borealis* phase (PSME/COCA-LIBO; Douglas-fir/bunchberry dogwood-twinflower phase)
- Pseudotsuga menziesii/Cornus canadensis* h.t.-*Vaccinium myrtillus* phase (PSME/COCA-VAMY; Douglas-fir/bunchberry dogwood-whortleberry phase)
- Picea/Vaccinium caespitosum* h.t. (PICEA/VACA; spruce/dwarf huckleberry)
- Picea/Linnaea borealis* h.t. (PICEA/LIBO; spruce/twinflower)
- Abies lasiocarpa/Vaccinium caespitosum* h.t. (ABLA/VACA; subalpine fir/dwarf huckleberry)
- Abies lasiocarpa/Calamagrostis canadensis* h.t.-*Vaccinium caespitosum* phase (ABLA/CACA-VACA; subalpine fir/bluejoint-dwarf huckleberry phase)
- Abies lasiocarpa/Linnaea borealis* h.t.-*Vaccinium scoparium* phase (ABLA/LIBO-VASC; subalpine fir/twinflower-grouse whortleberry phase)
- Abies lasiocarpa/Xerophyllum tenax* h.t.-*Vaccinium scoparium* phase (ABLA/XETE-VASC; subalpine fir/beargrass-grouse whortleberry phase)
- Abies lasiocarpa/Vaccinium globulare* h.t. (ABLA/VAGL; subalpine fir/blue huckleberry)
- Abies lasiocarpa/Vaccinium scoparium* h.t.-*Calamagrostis rubescens* phase (ABLA/VASC-CARU; subalpine fir/grouse whortleberry-pinegrass phase)
- Abies lasiocarpa/Vaccinium scoparium* h.t.-*Vaccinium scoparium* phase (ABLA/VASC-VASC; subalpine fir/grouse whortleberry-grouse whortleberry phase)
- Abies lasiocarpa/Carex geyeri* h.t.-*Carex geyeri* phase (ABLA/CAGE-CAGE; subalpine fir/elk sedge-elk sedge phase)
- Pinus contorta/Purshia tridentata* h.t. (PICO/PUTR; lodgepole pine/antelope bitterbrush)
- Pinus contorta/Vaccinium caespitosum* h.t. (PICO/LIBO; lodgepole pine/twinflower)
- Pinus contorta/Vaccinium scoparium* h.t. (PICO/VASC; lodgepole pine/grouse whortleberry)
- Pinus contorta/Calamagrostis rubescens* h.t. (PICO/CARU; lodgepole pine/pinegrass)
- Pinus contorta/Juniperus communis* h.t. (PICO/JUCO; lodgepole pine/common juniper)

(con.)

APPENDIX C (Con.)

Fire Group 8 - Dry, lower subalpine habitat types:

- Picea/Linnaea borealis* h.t. (PICEA/LIBO; spruce/twinflower)
Picea/Physocarpus malvaceus h.t. (PICEA/PHMA; spruce/mountain ninebark)
Picea/Smilacina stellata h.t. (PICEA/SMST; spruce/starry false Solomon's seal)
Abies lasiocarpa/Xerophyllum tenax h.t.-*Vaccinium globulare* phase (ABLA/XETE-VAGL; subalpine fir/beargrass-blue huckleberry phase)
Tsuga mertensiana/Xerophyllum tenax h.t. (TSME/XETE; mountain hemlock/beargrass)
Abies lasiocarpa/Vaccinium scoparium h.t.-*Thalictrum occidentale* phase (ABLA/VASC-THOC; subalpine fir/grouse whortleberry-western meadowrue phase)
Abies lasiocarpa/Clematis pseudoalpina h.t. (ABLA/CLPS; subalpine fir/virgin's bower)
Abies lasiocarpa/Arnica cordifolia h.t. (ABLA/ARCO; subalpine fir/heartleaf arnica)
Abies lasiocarpa/Carex geyeri h.t.-*Pseudotsuga menziesii* phase (ABLA/CAGE-PSME; subalpine fir/elk sedge-Douglas-fir phase)
Picea/Clintonia uniflora h.t.-*Clintonia uniflora* phase (PICEA/CLUN-CLUN; spruce/queencup beadlily-queencup beadlily phase)
Picea/Galium triflorum h.t. (PICEA/GATR; spruce/sweetscented bedstraw)
Abies lasiocarpa/Oplopanox horridum h.t. (ABLA/OPHO; subalpine fir/devil's club)
Abies lasiocarpa/Clintonia uniflora h.t.-*Clintonia uniflora* phase (ABLA/CLUN-CLUN; subalpine fir/queencup beadlily-queencup beadlily phase)
Abies lasiocarpa/Clintonia uniflora h.t.-*Aralia nudicaulis* phase (ABLA/CLUN-ARNU; subalpine fir/queencup beadlily-wild sarsaparilla phase)
Abies lasiocarpa/Clintonia uniflora h.t.-*Vaccinium caespitosum* phase (ABLA/CLUN-VACA; subalpine fir/queencup beadlily-dwarf huckleberry phase)
Abies lasiocarpa/Clintonia uniflora h.t.-*Xerophyllum tenax* phase (ABLA/CLUN-XETE; subalpine fir/queencup beadlily-beargrass phase)
Abies lasiocarpa/Clintonia uniflora h.t.-*Menziesia ferruginea* phase (ABLA/CLUN-MEFE; subalpine fir/queencup beadlily-menziesia phase)
Abies lasiocarpa/Galium triflorum h.t. (ABLA/GATR; subalpine fir/sweetscented bedstraw)
Abies lasiocarpa/Calamagrostis canadensis h.t.-*Calamagrostis canadensis* phase (ABLA/CACA-CACA; subalpine fir/bluejoint-bluejoint phase)
Abies lasiocarpa/Calamagrostis canadensis h.t.-*Galium triflorum* phase (ABLA/CACA-GATR; subalpine fir/bluejoint-sweetscented bedstraw phase)
Abies lasiocarpa/Linnaea borealis h.t. (ABLA/LIBO; subalpine fir/twinflower)
Abies lasiocarpa/Linnaea borealis h.t.-*Linnaea borealis* phase (ABLA/LIBO-LIBO; subalpine fir/twinflower-twinflower phase)
Abies lasiocarpa/Linnaea borealis h.t.-*Xerophyllum tenax* phase (ABLA/LIBO-XETE; subalpine fir/twinflower-beargrass phase)
Abies lasiocarpa/Menziesia ferruginea h.t. (ABLA/MEFE; subalpine fir/menziesia phase)
Tsuga mertensiana/Menziesia ferruginea h.t. (TSME/MEFE; mountain hemlock/menziesia)
Abies lasiocarpa/Alnus sinuata h.t. (ABLA/ALSI; subalpine fir/sitka alder)

Fire Group 10 - Cold, moist upper subalpine and timberline habitat types:

- Picea/Senecio streptanthifolius* h.t.-*Picea* phase (PICEA/SEST-PICEA; spruce/cleftleaf groundsel-spruce phase)
Picea/Juniperus communis h.t. (PICEA/JUCO; spruce/common juniper)
Abies lasiocarpa/Ribes montigenum h.t. (ABLA/RIMO; subalpine fir/mountain gooseberry)
Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium h.t. (ABLA-PIAL/VASC; subalpine fir-whitebark pine/grouse whortleberry)
Abies lasiocarpa/Luzula hitchcockii h.t.-*Vaccinium scoparium* phase (ABLA/LUHI-VASC; subalpine fir/smooth woodrush-grouse whortleberry phase)
Abies lasiocarpa/Luzula hitchcockii h.t.-*Menziesia ferruginea* phase (ABLA/LUHI-MEFE; subalpine fir/smooth woodrush-menziesia phase)
Abies lasiocarpa/Juniperus communis h.t. (ABLA/JUCO; subalpine fir/common juniper)
Tsuga mertensiana/Luzula hitchcockii h.t.-*Vaccinium scoparium* phase (TSME/LUHI-VASC; mountain hemlock/smooth woodrush-grouse whortleberry phase)
Tsuga mertensiana/Luzula hitchcockii h.t.-*Menziesia ferruginea* phase (TSME/LUHI-MEFE; mountain hemlock/smooth woodrush-menziesia phase)
Pinus albicaulis-Abies lasiocarpa h.t.'s (PIAL-ABLA h.t.'s; whitebark pine-subalpine fir)
Larix lyallii-Abies lasiocarpa h.t.'s (LALY-ABLA h.t.'s; subalpine larch-subalpine fir)
Pinus albicaulis h.t.'s (PIAL h.t.'s; whitebark pine)

(con.)

APPENDIX C (Con.)

Fire Group 11 - Warm, moist grand fir, western hemlock, and western redcedar habitat types:

Abies grandis/Xerophyllum tenax h.t. (ABGR/XETE; grand fir/beargrass)

Abies grandis/Clintonia uniflora h.t.-*Clintonia uniflora* phase (ABGR/CLUN-CLUN; grand fir/queencup beadlily-queencup beadlily phase)

Abies grandis/Clintonia uniflora h.t.-*Aralia nudicaulis* phase (ABGR/CLUN-ARNU; grand fir/queencup beadlily-wild sarsaparilla phase)

Abies grandis/Clintonia uniflora h.t.-*Xerophyllum tenax* phase (ABGR/CLUN-XETE; grand fir/queencup beadlily-beargrass phase)

Abies grandis/Linnaea borealis h.t.-*Linnaea borealis* phase (ABGR/LIBO-LIBO; grand fir/twinflower-twinflower phase)

Abies grandis/Linnaea borealis h.t.-*Xerophyllum tenax* phase (ABGR/LIBO-XETE; grand fir/twinflower-beargrass phase)

Thuja plicata/Clintonia uniflora h.t.-*Clintonia uniflora* phase (THPL/CLUN-CLUN; western redcedar/queencup beadlily-queencup beadlily phase)

Thuja plicata/Clintonia uniflora h.t.-*Aralia nudicaulis* phase (THPL/CLUN-ARNU; western redcedar/queencup beadlily-wild sarsaparilla phase)

Thuja plicata/Clintonia uniflora h.t.-*Menziesia ferruginea* phase (THPL/CLUN-MEFE; western redcedar/queencup beadlily-menziesia phase)

Thuja plicata/Oplopanax horridum h.t. (THPL/OPHO; western redcedar/devil's club)

Tsuga heterophylla/Clintonia uniflora h.t.-*Clintonia uniflora* phase (TSHE/CLUN-CLUN; western hemlock/queencup beadlily-queencup beadlily phase)

Tsuga heterophylla/Clintonia uniflora h.t.-*Aralia nudicaulis* phase (TSHE/CLUN-ARNU; western hemlock/queencup beadlily-wild sarsaparilla phase)

APPENDIX D: SCIENTIFIC NAMES OF PLANTS IN TEXT

Common name	Scientific name	Common name	Scientific name
Alder	<i>Alnus</i> spp.	Pacific yew	<i>Taxus brevifolia</i>
American trailplant	<i>Andenocaulon bicolor</i>	Paper birch	<i>Betula papyrifera</i>
American twinflower	<i>Linnaea borealis</i>	Parry rush	<i>Juncus parryi</i>
Antelope bitterbrush	<i>Purshia tridentata</i>	Pinegrass	<i>Calamagrostis rubescens</i>
Arrowleaf balsamroot	<i>Balsamorhiza sagittata</i>	Plains muhly	<i>Muhlenbergia cuspidata</i>
Arrowleaf groundsel	<i>Senecio triangularis</i>	Ponderosa pine	<i>Pinus ponderosa</i>
Ballhead sandwort	<i>Arenaria congesta</i>	Prickly currant	<i>Ribes lacustre</i>
Big sagebrush	<i>Artemisia tridentata</i>	Prince's pine	<i>Chimaphila umbellata</i>
Black cottonwood	<i>Populus trichocarpa</i>	Pyrola	<i>Pyrola</i>
Bluebunch wheatgrass	<i>Agropyron spicatum</i>	Quaking aspen	<i>Populus tremuloides</i>
Bluejoint	<i>Calamagrostis canadensis</i>	Queencup beadlily	<i>Clintonia uniflora</i>
Bluestem	<i>Andropogon</i>	Redosier dogwood	<i>Cornus stolonifera</i>
Bracken fern	<i>Pteridium aquilinum</i>	Richardson's geranium	<i>Geranium richardsonii</i>
Broadleaf arnica	<i>Arnica latifolia</i>	Rocky Mountain juniper	<i>Juniperus scopulorum</i>
Bunchberry dogwood	<i>Cornus canadensis</i>	Rocky Mountain maple	<i>Acer glabrum</i>
Canada violet	<i>Viola canadensis</i>	Ross sedge	<i>Carex rossii</i>
Chokecherry	<i>Prunus virginiana</i>	Rough fescue	<i>Festuca scabrella</i>
Cleftleaf groundsel	<i>Senecio streptanthifolius</i>	Russet buffaloberry	<i>Shepherdia canadensis</i>
Columbia bromegrass	<i>Bromus vulgaris</i>	Rusty menziesia	<i>Menziesia ferruginea</i>
Common snowberry	<i>Symphoricarpos albus</i>	Scouler willow	<i>Salix scouleriana</i>
Common beargrass	<i>Xerophyllum tenax</i>	Shrubby cinquefoil	<i>Potentilla fruticosa</i>
Common juniper	<i>Juniperus communis</i>	Sidebells shineleaf	<i>Pyrola secunda</i>
Conspicuous aster	<i>Aster conspicuus</i>	Sitka alder	<i>Alnus sinuata</i>
Creeping juniper	<i>Juniperus horizontalis</i>	Slender hawkweed	<i>Hieracium gracile</i>
Creeping Oregon grape	<i>Berberis repens</i>	Smooth woodrush	<i>Luzula hitchcockii</i>
Curlleaf mountain mahogany or curlleaf cercocarpus	<i>Cercocarpus ledifolius</i>	Solomon's seal	<i>Polygonatus pubescens</i>
Dampwoods blueberry	<i>Vaccinium globulare</i>	Snowbrush ceanothus	<i>Ceanothus velutinus</i>
Darkwoods violet	<i>Viola orbiculata</i>	Spreading dogbane	<i>Apocynum androsaemifolium</i>
Devil's club	<i>Oplopanax horridum</i>	Spruce	<i>Picea</i>
Douglas-fir	<i>Pseudotsuga menziesii</i>	Starry false Solomon's seal	<i>Smilacina stellata</i>
Dwarf huckleberry	<i>Vaccinium caespitosum</i>	Subalpine fir	<i>Abies lasiocarpa</i>
Dwarf mistletoe	<i>Arceuthobium</i>	Subalpine larch	<i>Larix lyallii</i>
Elk sedge	<i>Carex geyeri</i>	Sweetscented bedstraw	<i>Galium triflorum</i>
Engelmann spruce	<i>Picea engelmannii</i>	Sweetleaf arnica	<i>Arnica</i>
False Solomon's seal	<i>Smilacina racemosa</i>	Thimbleberry	<i>Rubus parviflorus</i>
Field horsetail	<i>Equisetum arvense</i>	Threelaf foamflower	<i>Tiarella trifoliata</i>
Grand fir	<i>Abies grandis</i>	Timber milkvetch	<i>Astragalus miser</i>
Greene mountainash	<i>Sorbus scopulina</i>	Twisted stalk	<i>Streptopus amplexifolius</i>
Grouse whortleberry	<i>Vaccinium scoparium</i>	Utah honeysuckle	<i>Lonicera utahensis</i>
Hairy goldenaster	<i>Chrysopsis villosa</i>	Virginia strawberry	<i>Fragaria virginiana</i>
Heartleaf arnica	<i>Arnica cordifolia</i>	Virgin's bower	<i>Clematis pseudoalpina</i>
Hollygrape	<i>Berberis</i>	Wartberry fairybells	<i>Disporum trachycarpum</i>
Idaho fescue	<i>Festuca idahoensis</i>	Wax currant	<i>Ribes cereum</i>
Junegrass	<i>Koeleria cristata</i>	Western hemlock	<i>Tsuga heterophylla</i>
Kinnikinnick	<i>Arctostaphylos uva-ursi</i>	Western larch	<i>Larix occidentalis</i>
Lady fern	<i>Athyrium felix-femina</i>	Western meadowrue	<i>Thalictrum occidentale</i>
Lewis mockorange	<i>Philadelphus lewisii</i>	Western rattlesnake plantain	<i>Goodyera oblongifolia</i>
Limber pine	<i>Pinus flexilis</i>	Western redcedar	<i>Thuja plicata</i>
Lodgepole pine	<i>Pinus contorta</i>	Western serviceberry	<i>Amelanchier alnifolia</i>
Manyleaf swampl laurel	<i>Kalmia polifolia</i>	Western snowberry	<i>Symphoricarpos occidentalis</i>
Mountain arnica	<i>Arnica latifolia</i>	Western white pine	<i>Pinus monticola</i>
Mountain deathcamas	<i>Zygadenus elegans</i>	Western wintergreen	<i>Gaultheria humifusa</i>
Mountain gooseberry	<i>Ribes montigenum</i>	White stone seed	<i>Lithospermum ruderales</i>
Mountain heath	<i>Phyllodoce empetrifomis</i>	White spirea	<i>Spiraea betulifolia</i>
Mountain hemlock	<i>Tsuga mertensiana</i>	White spruce	<i>Picea glauca</i>
Mountain lover	<i>Pachystima myrsinites</i>	Whitebark pine	<i>Pinus albicaulis</i>
Mountain ninebark	<i>Physocarpus malvaceus</i>	Whiteflower rhododendron	<i>Rhododendron albiglorum</i>
Mountain snowberry	<i>Symphoricarpos oreophilus</i>	Whortleberry	<i>Vaccinium myrtillus</i>
Mountain sweetroot	<i>Osmorhiza chilensis</i>	Wild sarsaparilla	<i>Aralia nudicaulis</i>
Oceanspray	<i>Holodiscus</i>	Woodrush	<i>Luzula hitchcockii</i>
		Yellow mountain heather	<i>Phyllodoce glandulifolia</i>

Scientific and common names are taken from Checklist of United States Trees (Native and Naturalized) (Little 1979) and National Handbook of Plant Names (USDA SCS 1981).

Fischer, William C.; Bradley, Anne F. Fire ecology of western Montana forest habitat types. General Technical Report INT-223. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1987. 95 p.

Provides information on fire as an ecological factor for forest habitat types in western Montana. Identifies Fire Groups of habitat types based on fire's role in forest succession. Describes forest fuels and suggests considerations for fire management.

KEYWORDS: fire ecology, forest ecology, forest fire, fire management, habitat types, forest fuels

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

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United States
Department of
Agriculture

Forest Service

Intermountain
Research Station

General Technical
Report INT-224



An Economic Evaluation of the Oak Creek Range Management Area, Utah

C. Arden Pope III
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RESEARCH SUMMARY

The Oak Creek Range Management Area was established in 1978 under the Intermountain Region's Range Validation Program to provide information about the overall cost effectiveness of range improvement practices within pinyon-juniper ecosystems. The project continued through 1985. Despite disruptions caused by two large wildfires, tens of thousands of acres of revegetation work was completed, several water development projects were completed, and many miles of fences were built. Forage available to livestock was increased, and the need for reductions in grazing on some allotments was eliminated. Project leaders and participants demonstrated a high level of commitment, competence, and cooperation. The project has considerable value as a demonstration area.

However, the project was not economically feasible. Given the high costs of implementing and managing the project and the relatively low value of the increased forage production, the costs of the project far exceeded its benefits to livestock production. Attempts to account for non-market benefits and refine cost and benefit estimates have limited impact on the overall lack of cost-effectiveness.

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INTRODUCTION

From 1970 to 1972, the Forest Service conducted a nationwide Forest-Range Environmental Study of current and potential rangeland productivity. Based on this study, in late 1973 the Forest Service decided to implement an accelerated range management program that included several "validation areas" for various ecosystems. The Oak Creek Management Area was established under this program in 1978 to provide information about the overall effectiveness of range improvement practices within pinyon-juniper ecosystems. The project emphasized the necessity of and benefits from coordinated planning and action between Federal, State, and local agencies, as well as private landowners. Despite disruptions caused by two large wildfires, including the much publicized "Oak City Fire," tens of thousands of acres of revegetation work was completed, several water development projects were completed, many miles of fences were built, and over 50,000 acres of fire rehabilitation effort was completed. In 1985, coordinators of the project were awarded the Secretary of Agriculture's Distinguished Service Award for the most notable conservation action in the Nation.

The general project plan of the Oak Creek Mountain Range Evaluation Area stated that "a basic premise for all the development work is that of cost-effectiveness where marketable and nonmarketable range outputs and costs are evaluated" (U.S. Department of Agriculture, undated). Project managers often interpret the term "cost-effectiveness" to mean the least-cost method of applying various treatments. They seldom equate it with economic efficiency in the traditional manner of economists. Using the Oak Creek management project as a significant and unique case study, this paper evaluates the economic impacts of range improvement practices in the pinyon-juniper ecosystem. Although the participation of the private landowners and ranchers was vital to any success of the project, the basic focus of this analysis is on the economic efficiency and benefits and costs of range improvement practices on the pinyon-juniper vegetative zone that, in the project area, is confined almost entirely to National Forest and Bureau of Land Management (BLM).

This paper first describes the project area and gives a brief review of the project. Next is a discussion of the applicability of benefit-cost analysis to evaluate range improvement projects on public land. This is followed by the general results of the benefit-cost analysis and the non-market benefits of the project. And finally, the basic conclusions of the analysis.

Popular names of plants and animals are used in the text. The appendix contains a list of both popular and scientific names.

PROJECT AREA

The Oak Creek Management Area encompasses approximately 316,600 acres. It is about 15 miles north of Fillmore, UT, in Millard and Juab Counties (see figs. 1 and 2). It includes 117,200 acres managed by the Forest Service, 109,800 acres of private land, 59,800 acres of BLM land, and 29,700 acres of State land (see fig. 2).

Approximately 80 ranchers own land or run cattle within the project area. Most have less than 50 head of cattle that they graze on public lands. Within and surrounding the area are relatively small farming and ranching communities. The nearest major metropolitan areas are Provo/Orem and Salt Lake City, approximately 100 to 150 miles to the north. In spite of being relatively remote, the Oak Creek Area receives over 10,000 user-days of sport hunting and fishing.

Topography is highly variable, ranging from desert-shrub flats at the 4,700-foot elevation through rolling foothills and benches to steep rocky peaks that exceed 9,700 feet. The climate is characterized by cold winters and mild summers. Average annual precipitation ranges from approximately 7 inches at the lower elevations to over 20 inches at the higher elevations. There is significant year-to-year variability in precipitation.

Five major native vegetation zones are within the project area (see fig. 3). **Aspen-conifer**—with Douglas-fir, white fir, subalpine fir, quaking aspen, and Engelmann spruce as the major plant species—is found in the highest elevations. At somewhat lower elevations is **mountain brush** with Gambel oak, big tooth maple, antelope bitterbrush, common chokecherry, alderleaf, slender wheatgrass, smooth brome, bluebells, and geraniums as the major plant species. In the lower foothills and benches, the predominant vegetative zone is **pinyon-juniper** with Utah juniper and pinyon as major plant species, as well as species similar to those found in the sagebrush-grass zone.

The vegetative zones found on the lower flat lands are **sagebrush-grass** with big sagebrush, antelope bitterbrush, serviceberry, cliffrose, deerbrush, wheatgrass, needle-and-thread, and Sandberg bluegrass as major plant species; and **desert shrub** with greasewood, shadscale, horsebrush, fourwing saltbush, winterfat, squirreltail, sand dropseed, and saltgrass as the major plant species. Much of the rolling bottomland and flat alluvial plains that spread out

below the foothills is used as farmland, both dry land and irrigated land.

A wide variety of wildlife species can be found in the area. They include mule deer, jackrabbits, coyotes, bobcats, mourning doves, chukar, red-tailed hawks, and blue grouse. Surface water within the project area is limited.

Oak Creek is the only perennial stream. Fool Creek, Dug-gins Creek, and Eightmile Creek run for only part of the year. Fish are found only in Oak Creek. Stream conditions are relatively poor for fish production due to highly variable stream flow. Rainbow trout are stocked in the stream during the fishing season by the Utah Division of Wildlife Resources.

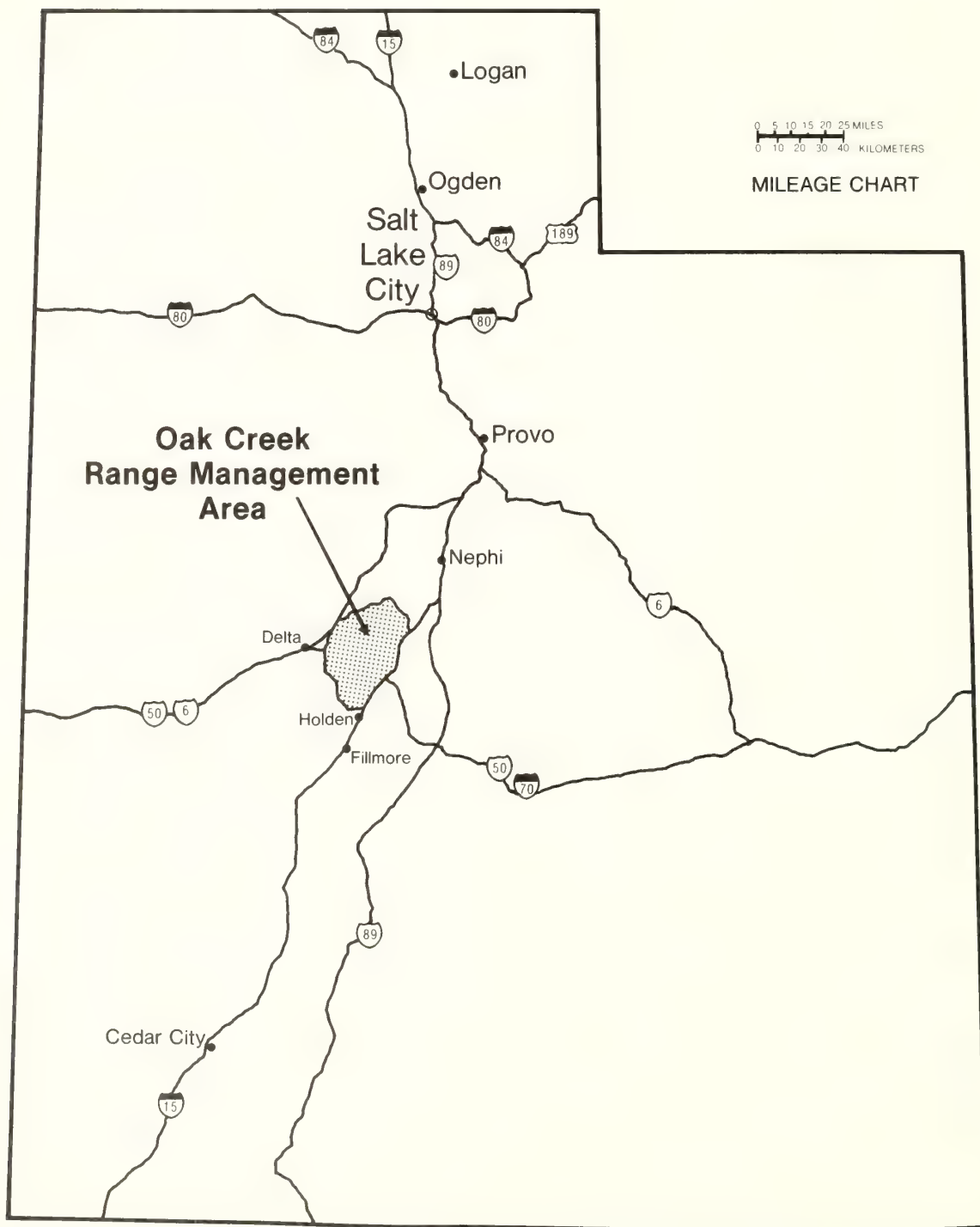


Figure 1—General location of Oak Creek Range Management Area.

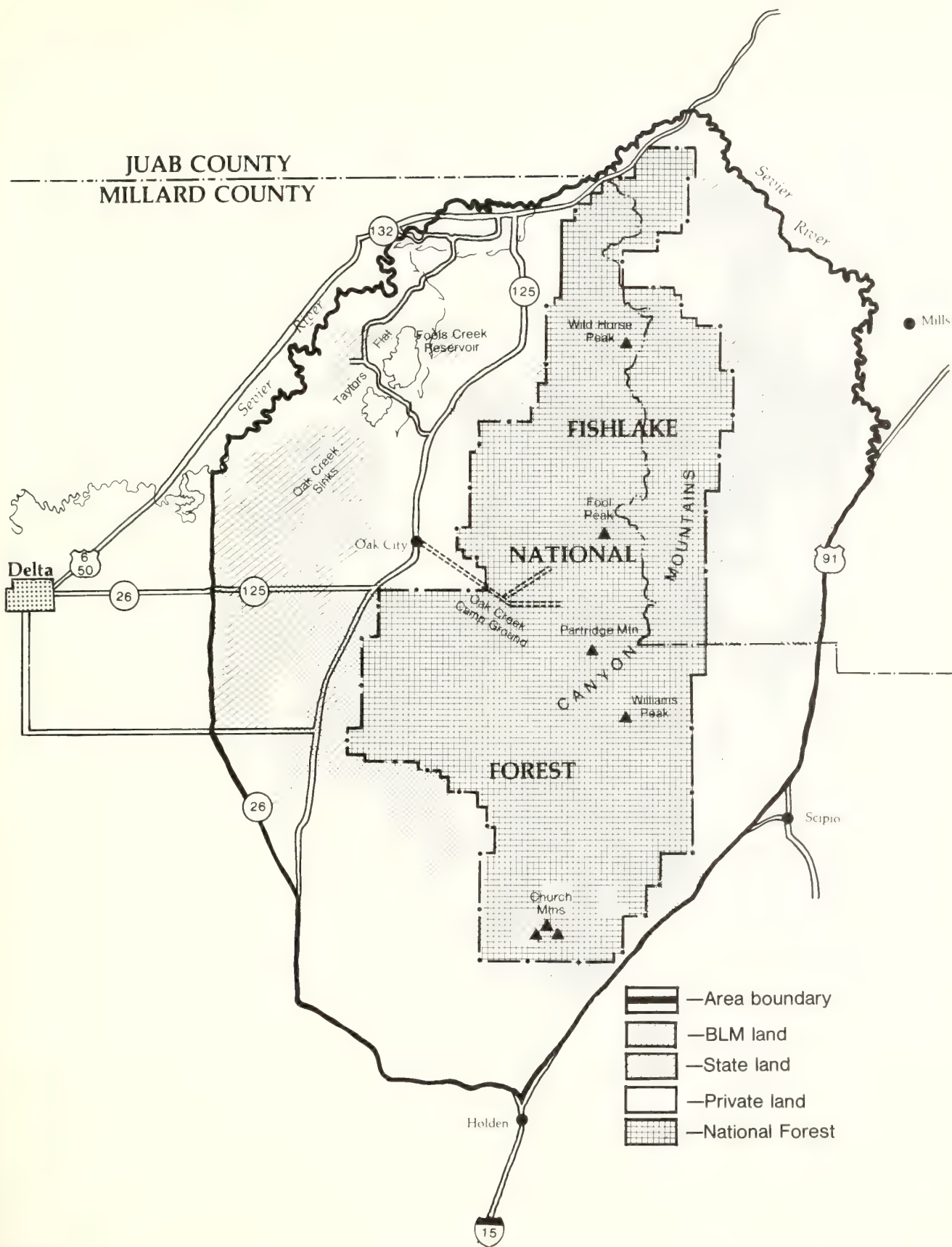


Figure 2—Jurisdictional areas.

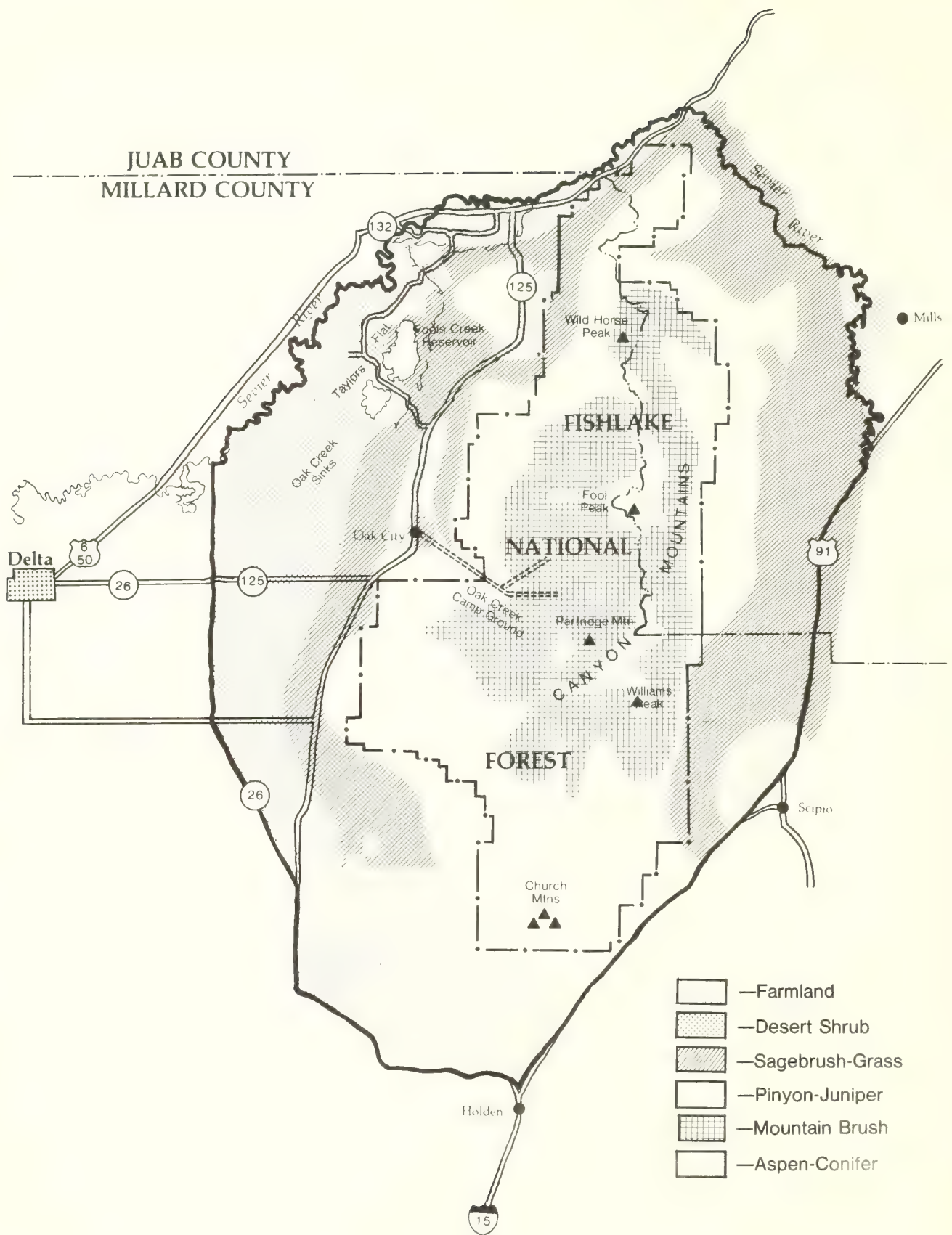


Figure 3—Vegetation zones.

HISTORY AND DESCRIPTION

Initially in 1973, the accelerated range management program as envisioned by the Forest Service was extremely ambitious. Several validation areas, often including various sites, were to be included. Baseline data and a variety of research projects dealing with vegetation, watershed conditions, wildlife habitat, socio-economic conditions, and other variables were to be compiled and completed. Only two actual projects of significant size and scope were established in the West. The first, the Oregon Range and Related Resources Validation Area, was started in 1976. In 1978, the Oak Creek Area was nominated by the Fillmore Ranger District, Fishlake National Forest, for inclusion in the Intermountain Region's Range Validation Program. The same year boundaries were delineated, initial funding levels were obligated, and range improvement projects were started. Initially called the "Oak Creek Validation Area," it was renamed "Oak Creek Mountain Range Evaluation Area" and finally changed to "Oak Creek Coordinated Resource Management and Planning Area." The project was to be completed by 1985.

The Forest Service assumed the lead role in coordinating the overall project. A project leader was assigned by the Forest Service and stationed at the Fillmore Ranger District office. Cooperators included the Bureau of Land Management, the Soil Conservation Service (SCS), the Agricultural Stabilization and Conservation Service (ASCS), the State of Utah, county commissioners, and private landowners. This group was facilitated through an executive and a steering committee. Cost-share funds were provided to ranchers in the project area through the ASCS, with the SCS providing technical assistance to private landowners.

Three types of range improvements were planned: (1) revegetation, (2) water development, and (3) fencing. The revegetation was to be done primarily through chaining and aerial seeding of the pinyon-juniper vegetation zone. Water development consisted almost entirely of piping water from available sources to a series of troughs. The fencing consisted of moving, building, and rebuilding fences to allow for the use of better grazing management.

Through 1981, the project proceeded mostly as scheduled. Then, from June 25 to July 31, lightning storms, coupled with dry weather conditions and high winds, caused fires that burned over 63,000 acres on the evaluation area (see fig. 4). One of the results of this fire was greatly increased funding. A great deal of revegetation work was completed—most for purposes of fire rehabilitation—along with much water development and fencing work. On-the-ground implementation of the project was put 2 to 3 years ahead of schedule. Many of the proposed range improvement projects on Federal and State land were completed as fire rehabilitation measures before they would have been approved as coordinated resource management plans. Areas of pinyon-juniper that had been burned were chained and seeded as originally planned. One large area that burned was BLM-administered land called the "Dust Bowl," which was primarily rolling hills or flat land supporting sagebrush-grassland. This area was seeded using rangeland drills. Almost 1,200 acres had to be reseeded later after severe windstorms blew out most of the germinated seedlings.

The fires threatened the small community of Oak City and caused some property damage. Approximately \$1.4 million was spent trying to control them. Even without the massive chaining, seeding, and water development project, the fires themselves would have had some positive effects on the range through controlling and "knocking back" large areas of pinyon-juniper vegetation.

A major impact of the fires, of particular significance for this study, was on the research phase of the evaluation project. Many potential studies, monitoring opportunities, and research possibilities were lost. Research was restricted to a much more limited basis than was stated in the project plan.

In 1982, funding and a work force available for the project were greatly reduced. In 1983, this and other range evaluation projects were eliminated from the Forest Service budget as part of general Federal budget reductions. The Intermountain Region continued to coordinate and support the project, but the research and evaluation portion of the project was greatly reduced and the project received its final title: "The Oak Creek Coordinated Resource Management and Planning Area."

In 1985, planned project work on Federal land was essentially completed. Completed water development and revegetation projects in relation to the Forest Service and BLM allotment boundaries are illustrated in figure 5. Approximately \$1.75 million had been spent on range improvement practices on National Forest and BLM lands. Cost-share funds channeled through the ASCS for work on private lands will continue.

APPLICATION OF BENEFIT-COST ANALYSIS

Benefit-cost analysis attempts to compare all of the benefits and costs associated with a given investment. It recognizes that most resources are scarce and should be allocated to meet the objectives of an individual, group of individuals, or the public at large. Inherent in economic analysis is the understanding that there are trade-offs in resource allocation decisions. If costs of a project are greater than benefits that are to be gained, then it is a questionable endeavor. Also, if greater returns for the same expenditures can be obtained elsewhere, the funds should be spent there. The major problems associated with applied benefit-cost analysis (as also with other tools of economic analysis) are those related to the difficulty of adding and comparing various benefits and costs. The most common way of doing this is to assign monetary values to all costs and benefits.

The benefit-cost approach has been widely used in analyzing public investment in range management, but it has its critics. Benefit-cost studies have often not favored public investments in range improvements. Moody, formerly with the ASCS, writes about the inadequacy of the cost-benefit ratio as a measure of the public interest. He quotes an anonymous reviewer's criticizing of "benefit-cost apologists." The reviewer suggests that the results rely "on the analyst's good judgment. . . which might as well be left to the public decision-maker (legislative or executive) where it always has rested rather than go through the quasi-scientific (really the 'pseudo' or 'mythical' scientific) hocus-pocus of benefit-cost" (Moody 1974).

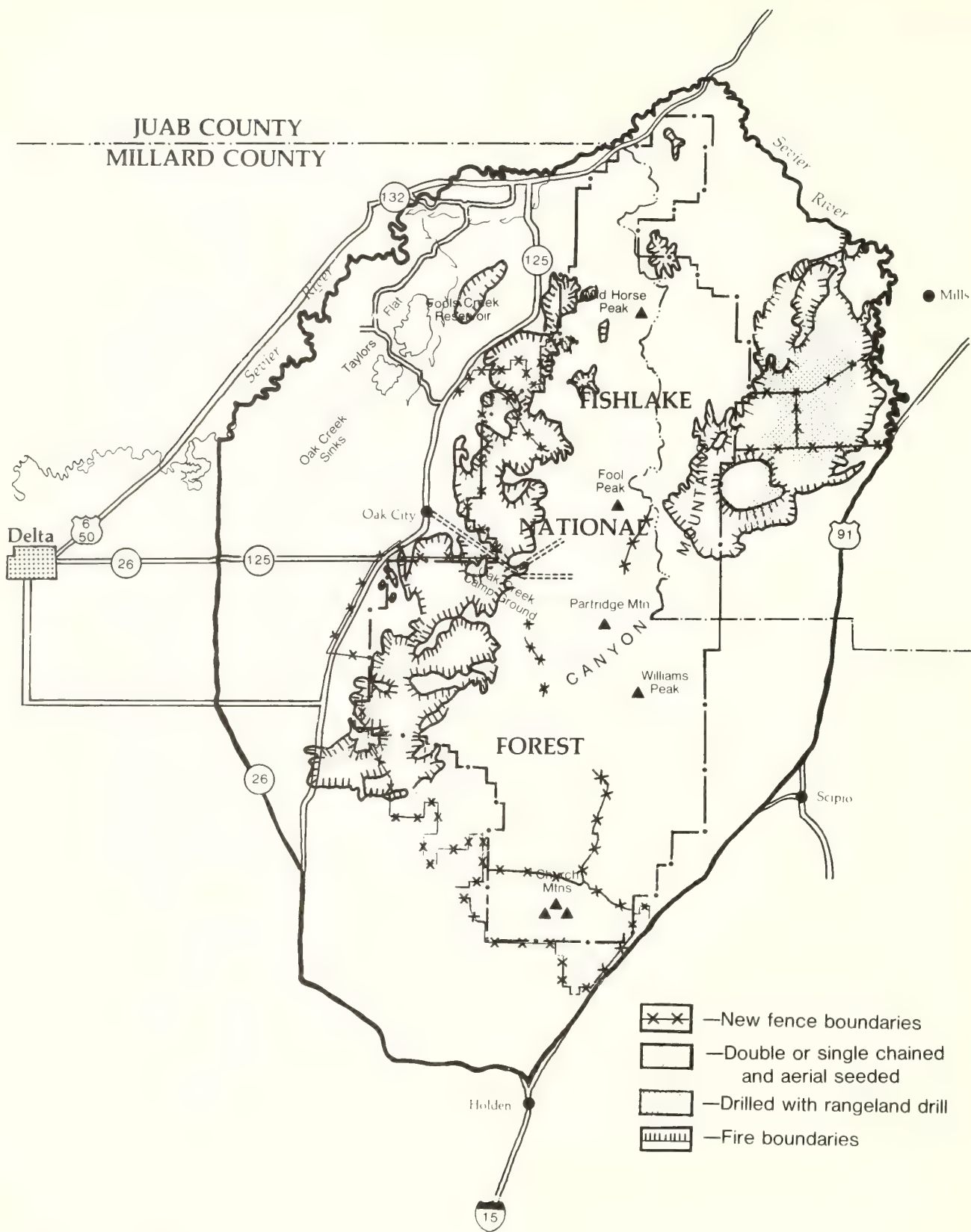


Figure 4—Fire boundaries.

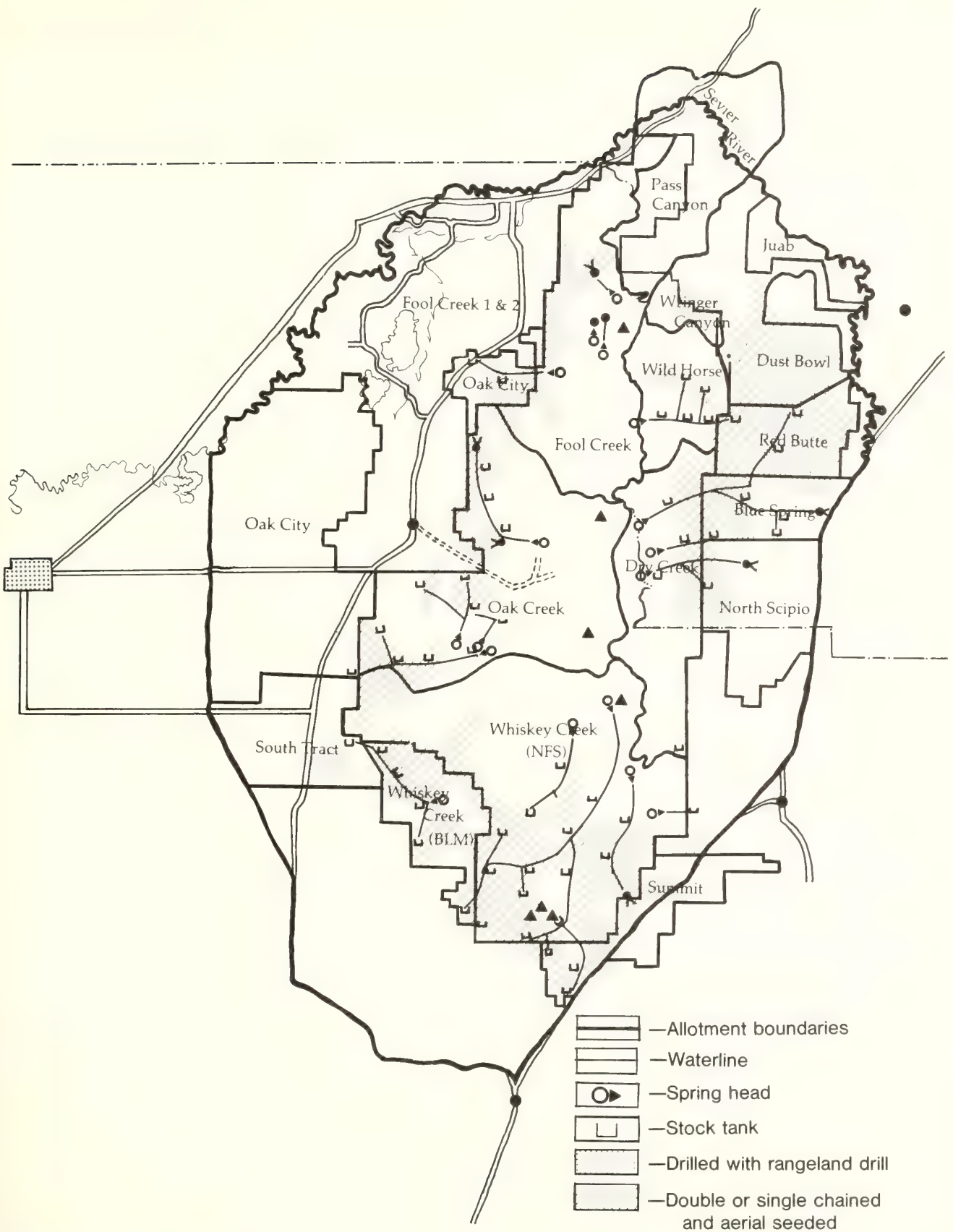


Figure 5—Improvement locations.

Of course, the question remains: Should public investment in range management be treated differently from private investment and should it become exempt from the rigors of economic analysis? Certainly public investment in range management can result in numerous nonmarket benefits that require good judgment to evaluate.

Although public investment in range projects is often motivated by noneconomic goals of government policy and various interest groups, this investment need not be exempt from economic analysis. Innumerable projects can be undertaken with the use of government funds—most of which would have the support of one interest group or another. The application of economic analysis, even with its inherent weaknesses, recognizes that resources, including public funds, are limited and should be allocated wisely. Benefit-cost analysis of a range-improvement project rarely, if ever, incorporates the value of all costs and benefits. But it can give a better understanding of how much we are paying for them. If measurable benefits do not outweigh measurable costs, it can then be asked whether unmeasurable benefits make up the difference or if the same public goals could have been accomplished through a less costly way.

RESULTS OF BENEFIT-COST ANALYSIS

Work completed on all seven Forest Service allotments in the area is included in the benefit-cost analysis. The two major areas of range improvement on BLM land are also included. In table 1, the numbers of acres, cattle, permit-

tees, and AUM's for each of the areas are given. Table 2 reports the number of acres of revegetation, and the direct costs of revegetation work, water development, fencing, and fire rehabilitation. All of the data in tables 1 and 2 were compiled from information provided by Forest Service and BLM records.

Table 2 does not include overhead costs. Forest Service overhead costs of the project are estimated at over \$287,000. The biggest item in these overhead costs was the project leader's salary. Other items include clerical help, use of pickup truck, other transportation costs, utilities, and building cleaning. All of these costs are prorated. Because of lack of reliable cost data, the overhead costs do not include any costs of buildings or building maintenance or any overhead cost for the BLM and other cooperators.

The calculation of monetary costs of the project is relatively straightforward; estimation of the value of the benefits is more difficult. Estimated net gains in AUM's resulting from the project are reported in table 3. These gains include not only increases in AUM's that resulted from the project, but also the mitigation or prevention of decreases that would have occurred had the project not been undertaken. For example, before the project there was to be a proposed average 35.5 percent reduction of AUM's on the Forest Service allotments. Following the project, AUM's available for livestock on National Forest land increased by approximately 22 percent. Both the avoided reductions and the actual increases in AUM's are included in the estimated net gains in AUM's from the project.

Table 1—Summary of areas of public land included in economic evaluation

Areas ¹	Total acres	Suitable acres ²	Cattle before project	Permittees	AUM's ³ before project
Dry Creek (FS)	14,929	5,102	290	8	598
Fool Creek (FS)	23,273	6,054	158	5	532
Oak Creek (FS)	31,378	8,367	340	11	804
Pass Canyon (FS)	2,823	1,403	40	1	300
Whiskey Creek (FS)	36,925	25,987	481	12	2,243
Wild Horse (FS)	7,313	2,954	278	2	834
Wringer Canyon (FS)	2,946	1,142	91	2	182
Subtotal (FS)	119,587	51,009	1,678	40	5,493
Dust Bowl (BLM)	25,587	—	437	6	1,865
Whiskey Creek (BLM)	5,025	—	39	4	184
Subtotal (BLM)	30,612	—	476	10	2,049
Grand Total (FS and BLM)	150,199	51,009	2,154	50	7,542

¹Each of the areas corresponds with allotment boundaries of the same name except Dust Bowl, which includes Blue Springs, Dust Bowl, Red Butte, and North Scipio allotments.

²Acres suitable for grazing of cattle. It is estimated that over 75 percent of the BLM land is suitable for grazing.

³Animal unit months (AUM) are, in practice, defined differently by the BLM and the Forest Service. The BLM defines an AUM as the forage required to sustain one mature cow with or without a calf for one full month and uses this measure (AUM) for purposes of billing for grazing fees. The Forest Service defines an animal month (AM) the same as the BLM defines an AUM and for the purposes of billing for grazing fees uses animal months. If the cow has a calf, the Forest Service adjusts AM by a conversion factor of 1.32 to get AUM's. For the purposes of this report, the BLM's definition of an AUM is used.

Table 2—Acres of revegetation and dollars spent on Oak Creek Management Project

Areas ¹	Acres of revegetation	Dollars spent				Total ²
		Revegetation	Water development	Fencing	Fire rehabilitation	
Dry Creek (FS)	2,100	63,925	32,462	32,740	15,353	144,480
Fool Creek (FS)	1,750	59,184	26,448	24,892	2,890	113,414
Oak Creek (FS)	4,260	104,729	66,795	66,211	32,291	270,026
Pass Canyon (FS)	0	0	0	3,700	0	3,700
Whiskey Creek (FS)	8,025	251,171	111,021	78,662	0	440,854
Wild Horse (FS)	495	11,995	14,550	8,000	0	34,545
Wringer Canyon (FS)	175	4,241	0	0	0	4,241
Subtotal (FS)	16,805	495,245	251,276	214,205	50,534	1,011,260
Dust Bowl (BLM)	11,041	194,912	31,992	56,330	—	283,234
Whiskey Creek (BLM)	5,476	141,677	13,119	14,765	—	169,561
Subtotal (BLM)	16,517	336,589	45,111	71,095	—	452,795
Grand Total (FS and BLM)	33,322	831,834	296,387	285,300	50,534	1,464,055

¹Each of the areas correspond with allotment boundaries of the same name except Dust Bowl, which includes Blue Springs, Dust Bowl, Red Butte, and North Scipio allotments.

²Excluding all administrative and overhead costs

Table 3—Estimated net gains in AUM's, estimated value of AUM's, and benefit-cost (B/C) ratio for Oak Creek Management Project

Areas ¹	Estimated net gain in AUM's from project ²	Capitalized value of added grazing fee revenue ³	Capitalized value of AUM's added by project	B/C ⁴ ratio I	B/C ⁵ ratio II
Dry Creek (FS)	287	5,166	24,395	0.04	0.17
Fool Creek (FS)	372	6,696	31,620	.06	.28
Oak Creek (FS)	949	17,082	80,665	.06	.30
Pass Canyon (FS)	0	0	0	0	0
Whiskey Creek (FS)	1,480	26,640	125,800	.06	.29
Wild Horse (FS)	63	1,134	5,355	.03	.16
Wringer Canyon (FS)	0	0	0	0	0
Subtotal (FS)	3,152	56,736	267,920	.06	.26
Dust Bowl (BLM)	1,994	35,892	169,490	.13	.60
Whiskey Creek (BLM)	340	6,120	28,900	.04	.17
Subtotal (BLM)	2,334	42,012	198,390	.09	.44
Grand Total (FS and BLM)	5,486	98,748	466,310	.07	.32

¹Each of the areas correspond with allotment boundaries of the same name except Dust Bowl, which includes Blue Springs, Dust Bowl, Red Butte, and North Scipio allotments.

²Including projected losses to occur without project.

³ $1.35/0.075 \times$ (estimated net gain in AUM's from project). Note that these values are capitalized and not annual values.

⁴(Value of added grazing fee income)/(total dollars spent).

⁵(Value of AUM's added by project)/(total dollars spent).

Three sets of price data are used to estimate the value of an AUM within the project area. The first set of prices is accepted bid prices for grazing on State of Utah Division of Wildlife Resources land. The State lands, similar to those in the project area, that are included in an open bidding process are used to calculate average bid prices for each year. Most of this land is in pinyon-juniper eco-systems. Table 4 presents these data. Note that average accepted bid prices reported in table 4 are nearly equal to the appraised market value of grazing on public range-lands on price areas 4 and 5 as reported in the "1985 Grazing Fee Review and Evaluation" (U.S. Department of Agriculture 1985).

The second set of prices is from information on transfers of grazing permits from the Fillmore Ranger District. The Forest Service does not actually allow for direct transfers of permits between ranchers. The Forest Service has always maintained the right to make adjustments or even cancel permits to properly manage the range or forest land for a number of uses, only one of which is livestock grazing. When a rancher sells livestock or base property, the rancher waives the grazing permit back to the Government who in turn may reissue to the purchaser. By long-standing precedent, however, this permit is usually reissued to the purchaser of the livestock, base property, or both. Any value that the permit may have is incorporated into the sales price of the livestock, base property, or both. The permit values are recognized by ranchers and, in practice, can be and are bought and sold.

All transfers of reissuances of grazing permits from the Fillmore Ranger District that occurred from 1978 to June 1985 were obtained. These were transfers of permits on National Forest land within or directly surrounding the project area. In this period, 38 transfers occurred. During July 1985, buyers of these permits were contacted to establish the actual amount paid for the permits alone. Of the 38 transfers, 24 were bonafide transactions where the permits were actually bought and sold and the cost of the permits could be verified. All 24 transactions involved only the buying and selling of permits and cattle. On nine of the transfers, the cost of the permits could not be verified

because the whole ranch was sold with no reliable breakdown of cost of permits, the buyer couldn't remember or didn't know the breakdown between cows and permits, or the transaction occurred between family members at a "less than arm's length" deal. Five of the buyers could not be contacted. All of the ranchers contacted willingly verified the transaction and provided the cost of the permits when it was available.

The cost of permits on an AUM basis ranged from \$29.70 to \$95.45 with an average of \$57.29. The average costs of the permits on an AUM basis for 1978 to 1985 are given in table 5. They compare closely with 1983 public permit values in Utah as observed in the "1985 Grazing Fee Review and Evaluation" (U.S. Department of Agriculture 1985). That report showed average permit value per AUM ranging from a low of \$42 to a high of \$100 with an average of \$50.

Table 5—Average price of grazing permits in the Fishlake National Forest, Fillmore Ranger District, 1978 to 1985

Year	Number of observations	Number of AUM's	Average permit price (\$/AUM)
1978	3	1,339.5	42.93
1979	3	469.68	63.61
1980	2	335.33	51.14
1981	2	216.83	72.06
1982	4	709.33	66.19
1983	4	732.83	69.73
1984	4	211.02	57.34
1985	2	76.33	53.45
Total	24	4,090.85	57.29

The final set of forage values used is the established grazing fee of the BLM and Forest Service. The fees charged from 1978 to 1985 are reported in table 6. When these fees are subtracted from the market value of an AUM as estimated by average accepted bid prices, the value of an AUM not captured by grazing fees is estimated. When this value is capitalized it approximates the value of a grazing permit. To get an indication of what would be a reasonable capitalization rate, table 6 reports the capitalization rates that would result in the average price of all grazing permits for each year.

Based on the available information, various values of an AUM can be estimated, depending on the assumptions used. (This is discussed further in Wagstaff and Pope, in preparation.) For example, if we assume that effects of the project extend into perpetuity (their effects are estimated more likely to last a maximum of 50 years), the average accepted bid price for similar grazing on State land can be capitalized. If the average 1985 accepted bid price of \$6.41 is capitalized by 10, 7.5, and 4 percent, it yields capitalized values of an AUM equal to \$64, \$85, and \$160, respectively. Another estimate of the value of an AUM can be obtained by taking the average AUM price of a grazing permit and adding to that the capitalized value

Table 4—Average accepted bid prices per AUM for livestock grazing on Utah Division of Wildlife Resources land, 1978 to 1985

Year	Number of areas	AUM's	Total dollars	Average annual bid (\$/AUM)
1978	20	3,846.5	20,312.72	5.28
1979	25	4,367.5	20,727.73	4.75
1980	20	3,902	16,657.67	4.27
1981	18	3,129	17,005.95	5.44
1982	23	3,864	24,066.65	6.23
1983	20	3,841	21,942.93	5.71
1984	19	4,015	26,373.20	6.57
1985	28	4,543	29,121.88	6.41
Average	—	3,938.5	22,026.09	5.59

Source: Utah Division of Wildlife Resources (1978-1985).

Table 6—Grazing fee per AUM for Forest Service and BLM and capitalization rate, 1978 to 1985

Year	Grazing fee		Capitalization rate ¹
	FS	BLM	
	----- Dollars -----		Percent
1978	1.60	1.51	8.68
1979	1.93	1.89	4.46
1980	2.41	2.36	3.69
1981		2.31	4.34
1982		1.86	6.60
1983		1.40	6.18
1984		1.37	8.89
1985		1.35	9.47
Average		1.77	6.67

¹This value is obtained by subtracting the grazing fee value in this table from the average accepted bid price in table 4 and dividing the results by the average price of grazing permits from table 5.

of the grazing fee. The average AUM price of a grazing permit from 1978 to 1985 equals \$57. The average grazing fee during this same period equals \$1.77. Capitalizing \$1.77 by 10, 7.5, and 4 percent and adding those values to \$57 yields estimates of AUM values of \$75, \$81, and \$101, respectively. Using available data and a variety of reasonable assumptions yields estimates of AUM values ranging from \$50 to \$160.

For the purposes of this analysis, an estimate of \$85 is used as the capitalized value of an AUM. Multiplying it by the net gain in AUM's gives the value of project benefits to livestock production as reported in table 3. The benefit-cost ratios are also reported in table 3. Because the direct costs of the project greatly exceeded the benefits, the benefit-cost ratio overall for the project was only 0.32. When a conservative estimate of overhead costs is also included, the ratio drops to 0.27, indicating that the total costs of the project were nearly four times the estimated benefits to livestock production.

These basic results are not sensitive to reasonable changes in assumptions or methodology. Fine-tuning the assumptions or methodology or both tends to be even less favorable, in terms of economic feasibility, to the project. For example, if all costs and benefits are adjusted for inflation and a finite life of the project is used, then measured benefits are reduced and costs are increased. Most of the benefits of the project were not experienced until 1984 to 1985 or beyond. Many of the costs, however, were incurred up to 7 years before. Adjusting all costs into 1984 dollars using the gross national product (GNP) implicit price deflator results in real costs in 1984 dollars being approximately 15 percent higher than nominal dollars used in this study.

Also, as table 7 shows, well above-normal moisture conditions were experienced in the project area each year between 1980 and 1985. On the average, precipitation in the areas exceeded normals by nearly 50 percent. Although it is nearly impossible to separate the effects, given available data, it is likely that these several back-to-back years of relatively good moisture conditions would have improved forage production even without the project.

Table 7—Annual precipitation for Oak City, Scipio, and Fillmore, UT, Stations¹

Year	Oak City	Scipio	Fillmore	Average
1970	12.11	12.99	14.04	13.05
1971	15.10*	13.39	16.00	14.83
1972	11.82	15.19*	15.95	14.32
1973	12.67	14.33	17.66*	14.89
1974	7.74	10.26	12.32	10.11
1975	15.58*	16.68**	14.95	15.74*
1976	8.25	8.64	8.66	8.52
1977	8.73	7.94	10.00	8.89
1978	19.16***	16.29**	16.79*	17.41**
1979	11.36	11.47	13.85	12.23
1980	17.99***	19.12***	17.77*	18.29**
1981	16.79**	15.87**	18.57*	17.08**
1982	18.26***	20.01***	21.27***	19.85***
1983	20.23***	26.03***	25.33***	23.86***
1984	19.37***	18.22***	20.55**	19.38***
1985	² 13.68	² 13.71	² 17.34	² 14.91
Normal	12.15	12.51	14.51	13.06

Source: National Oceanic and Atmospheric Administration.

* indicates that the precipitation value is more than 15 percent above normal; ** indicates more than 30 percent above normal; and *** indicates more than 45 percent above normal.

²December precipitation values for 1985 were not yet available. Precipitation values for 1985 include only the first 11 months but are still above annual normals. If normal December precipitation is assumed, the average total precipitation for these three stations would be over 20 percent above normal.

Finally, the estimate of \$85 for the value of an AUM on the project area may be a little generous. It is liberally based on data that have both the annual and capitalized value of an AUM, for the most part, slightly higher than even the "1985 Grazing Fee Review and Evaluation" (U.S. Department of Agriculture 1985). This report has been criticized mostly by ranchers and ranching organizations as having exaggerated AUM values. They suggest that the current grazing fee more closely reflects the actual value of an AUM on Forest Service and BLM range. This, of course, would imply that the capitalized value of an AUM is less than \$20 and would further reduce the measured benefits of this project. Nevertheless, the general results of the analysis are not sensitive to reasonable estimates of AUM values. If overhead costs are included, the average value of an AUM would have to be over \$300—three and a half times the value used in this analysis—to make the project economically feasible on the basis of increased livestock production alone.

For the most part, the results of this case study show that the incremental benefits of either revegetation or water development projects did not cover their respective incremental costs. One exception is on the BLM's Dust Bowl area. It is unlikely that the chaining and seeding of the pinyon-juniper was economically feasible on this area, even though much of the area is relatively level, is within the sagebrush-grass vegetative zone, and did not require chaining. After the fire swept the area in 1981, it was seeded using a rangeland drill. Because of severe wind erosion that took place in the spring of 1982, nearly 1,200

acres had to be redrilled. Forage available for livestock has increased dramatically. On the range that did not require chaining, and could be drilled with a rangeland drill, the benefits to livestock production nearly outweigh the costs.

NONMARKET BENEFITS

From a range management project of this scale should come important intangible benefits. For example, the project may have had significant impacts on wildlife in the area. Table 8 shows that the annual value of wildlife for hunting and fishing on the Oak Creek deer unit (a unit that closely corresponds to the Oak Creek Management Area) equals an estimated \$242,848. This is much larger than the annual value of forage for livestock production on public land in the area. Before the project there were only about 7,542 AUM's on public land. The value of this forage is liberally estimated to equal \$48,080 on an annual basis.

Given the nature of the area, wildlife biologists doubt that any significant increases in wildlife values resulted from the project. With respect to big game—almost exclusively mule deer—summer range is the limiting factor. The project did little or nothing to improve summer range conditions for mule deer. The chaining and seeding work did improve winter range for mule deer, but the increase in livestock numbers, and the greater dispersion of livestock made possible through water development, probably offset any potential for significant benefits to mule deer (personal communication with Marion B. Cherry, wildlife biologist, Fillmore Ranger District, Fishlake National Forest, and Verdon Durfey, game biologist for Southern Region of the Utah Division of Wildlife Resources). Others close to the project suggest that big game may respond positively to the project over a long period (personal communication with Ronald S. Wilson, District Ranger,

Fillmore District). Impacts of the project on small and upland game were mixed (Cherry 1982).

The conclusions of the wildlife biologists are supported by deer harvest trend data in the Oak Creek deer unit (Utah Division of Wildlife Resources 1972-1985). In 1975, the unit was restricted to buck hunting only. The number of bucks harvested gradually rose from 218 in 1975 until it peaked at 693 in 1983. The percentage of successful hunters also rose from a low in 1975 of 13 percent to a high in 1982 of 48 percent. In 1984, the buck harvest fell to 514 and hunter success dropped to 29 percent. In an attempt to upgrade the deer herd, the Oak Creek deer herd unit was restricted to bucks with three points or better in 1985. The harvest dropped to 158 animals and the success rate was a mere 7.5 percent. Although several factors influence the deer herd in the project area, available information provides little evidence that the project made important contributions to wildlife values.

There are over 10,000 user days of outdoor recreation in the form of hunting and fishing (see table 8). No data are available on the number of days of dispersed nonconsumptive recreation. However, given the building of more fences, the tapping of natural springs for livestock water, and the increased grazing of cattle, it is doubtful that the impacts of the project on dispersed, consumptive, and non-consumptive recreation are positive. Also, impacts on watershed values of the area were not measured, although reseeding in the Dust Bowl after the fire did reduce wind erosion.

One objective of the project was to enhance or stabilize the incomes of the ranchers involved. The project increased the number of AUM's available to specific ranchers. Because the annual value of those AUM's is greater than grazing fees, the project created a significant benefit to the specific ranchers involved. Current users of public grazing are concerned about any changes in grazing levels or fees. Changes in the level of allowable grazing or in the annual grazing fee affect the equity position of their ranches. To the extent that this project eliminated the need for reductions in grazing levels, the equity positions of the ranchers were maintained. To the extent that the project enhanced grazing levels, it enhanced their equity position.

It must be noted, however, that excluding cost-sharing funds channeled through the ASCS, approximately \$1.75 million was spent. The present value of returns to the government from grazing fees is estimated at less than \$100,000. The present value of benefits to the ranchers in terms of preserved and enhanced incomes and equity positions is less than \$400,000.

Table 8—Annual value of wildlife for hunting purposes on the Oak Creek deer herd unit (#53), Fillmore Ranger District, Fishlake National Forest¹

Factor	User days ²	Average value per day ³	Total value
Big game hunting ⁴	6,646	\$23.10	\$153,523
Small and upland game hunting	3,000	26.80	80,400
Sport fishing	500	17.85	8,925
Total ⁵	10,146	—	242,848

¹These data are estimates obtained from an unpublished report, dated May 6, 1985, prepared by Marion B. Cherry, wildlife biologist, Fillmore Ranger District, Fishlake National Forest, and from personal communication with Cherry.

²User days are defined as 12-hour days.

³These values are substantially lower than those used by Idaho Fish and Game and the Washington Game Department.

⁴Hunters of big game with primitive weapons and on antlerless hunts are not included.

⁵Note that these are annual values and cannot be directly compared with the capitalized values in table 3. If the total value figure of \$242,848 is capitalized by 7.5 percent as are the values for AUM's, the capitalized value of wildlife for hunting would be over \$3 million.

CONCLUSIONS

In some ways the Oak Creek Range Management Project was a success. Forage available to livestock was increased, and the need for reductions in AUM's on some allotments was eliminated. To meet this end, project leaders and other participants demonstrated a high level of competence and cooperation. There was considerable value in having this project as a demonstration area for

range improvement and especially as a coordinated planning and development area. The value of the knowledge and experience gained from this project is not easily estimated. The project, however, based on comparison of costs and measurable benefits, simply was not economically justifiable. Although there is limited information about nonmarket costs and benefits associated with the project, the extent to which the costs exceeded even liberal estimates of benefits suggests that attempts to refine cost and benefit estimates would not change this conclusion.

It is also difficult to justify the project on the grounds that it met certain other public goals related to supporting local ranchers and communities. To do so implies there was not a more cost-effective means to meet these goals or that the goals were worth the differences between measurable costs and benefits. This project is questionable on both counts.

The public land within the Oak Creek Management Area is of particular interest because a superficial examination of the land suggests that it has little value except for its use in livestock production. The land is far removed from major metropolitan areas and is relatively desolate compared to other mountain ranges in the Intermountain West. Closer examination, however, indicates that the annual value of the area for outdoor recreation, primarily hunting, may be several times as large as the annual value of the forage for livestock production. Future management of such areas needs to take into account changing economic conditions that include relatively low beef prices, high costs of beef production on public lands, and an ever-growing demand for hunting, camping, wildlife and wildlands preservation, and other such uses of public land.

REFERENCES

- Cherry, M. B. The effects of pinyon-juniper chaining on wildlife of the Fillmore Ranger District, Fishlake National Forest. Logan, UT: Utah State University; 1982. 114 p. M.S. thesis.
- Moody, R. E. Inadequacy of the benefit-cost ratio as a measure of the public interest. *American Journal of Agricultural Economics*. 56(1): 188-191; 1974.
- National Oceanic and Atmospheric Administration. Climatological data, Utah. Washington, DC: National Oceanic and Atmospheric Administration; various issues, 1970-1985.
- U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management. 1985 grazing fee review and evaluation. Washington, DC: U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management; 1985. 99 p.
- U.S. Department of Agriculture, Forest Service, Intermountain Region. General project plan, Oak Creek mountain range evaluation area. Ogden, UT; undated. 65 p. Unpublished report.
- Utah Division of Wildlife Resources. Utah big game harvest book. Salt Lake City, UT: Utah Division of Wildlife Resources; 1972-1985.
- Utah Division of Wildlife Resources. Grazing on division land. 1978-1985. Unpublished summaries of accepted bid prices for grazing on State of Utah Division of Wildlife Resources land. [Obtained through personal communication with John Fairchild, Division of Wildlife Resources, Salt Lake City, UT.]
- Wagstaff, F. J.; Pope, C. A. Finding the appropriate forage value of analyzing the feasibility of public range improvements. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; [in preparation].

APPENDIX: POPULAR AND SCIENTIFIC NAMES OF PLANTS, MAMMALS, AND BIRDS DISCUSSED IN THIS PUBLICATION

Plants		Plants	
Common name	Scientific name	Common name	Scientific name
Alderleaf	<i>Cercocarpus montanus</i>	Quaking aspen	<i>Populus tremuloides</i>
Antelope bitterbrush	<i>Purshia tridentata</i>	Saltgrass	<i>Distichlis stricta</i>
Big sagebrush	<i>Artemisia tridentata</i>	Sand dropseed	<i>Sporobolus cryptandrus</i>
Bigtooth maple	<i>Acer grandidentatum</i>	Sandberg bluegrass	<i>Poa sandbergii</i>
Bluebells	<i>Mertensia</i> spp.	Serviceberry	<i>Amelanchier alnifolia</i>
Cliffrose	<i>Cowania mexicana</i>	Shadscale	<i>Atriplex confertifolia</i>
Common chokecherry	<i>Prunus virginiana</i>	Slender wheatgrass	<i>Agropyron trachycaulum</i>
Deerbrush	<i>Ceanothus velutinus</i>	Smooth brome	<i>Bromus inermis</i>
Douglas-fir	<i>Pseudotsuga menziesii</i>	Squirreltail	<i>Sitanion hystrix</i>
Engelmann spruce	<i>Picea engelmannii</i>	Subalpine fir	<i>Abies lasiocarpa</i>
Fourwing saltbush	<i>Atriplex canescens</i>	Utah juniper	<i>Juniperus osteosperma</i>
Gambel oak	<i>Quercus gambelii</i>	Wheatgrass	<i>Agropyron cristatum</i> ,
Geranium	<i>Geranium richardsonii</i>		<i>Agropyron intermedium</i> ,
Greasewood	<i>Sarcobatus vermiculatus</i>		<i>Agropyron smithii</i> ,
Horsebrush	<i>Tetradymia canescens</i>		<i>Agropyron spicatum</i> ,
Needle-and-thread	<i>Stipa comata</i>		<i>Agropyron trachycaulum</i>
Pinyon	<i>Pinus edulis</i>	White fir	<i>Abies concolor</i>
Pinyon-juniper	<i>Pinus monophylla</i> , <i>Pinus edulis</i> , <i>Juniperus osteosperma</i> , <i>Juniperus scopulorum</i> , <i>Juniperus monosperma</i> , <i>Juniperus communis</i> , <i>Juniperus virginiana</i>	Winterfat	<i>Eurotia lanata</i>

Birds		Mammals	
Common name	Scientific name	Common name	Scientific name
Blue grouse	<i>Dendragapus obscurus</i>	Antelope jackrabbit	<i>Lepus alleni</i>
Chukar	<i>Alectoris graeca</i>	Blacktail jackrabbit	<i>Lepus californicus</i>
Mourning dove	<i>Zenaidura macroura</i>	Bobcat	<i>Lynx rufus</i>
Red-tailed hawk	<i>Buteo jamaicensis</i>	Coyote	<i>Canis latrans</i>
		Mule deer	<i>Odocoileus hemionus</i>
		Whitetail jackrabbit	<i>Lepus townsendii</i>

Pope, C. Arden, III; Wagstaff, Fred J. 1987. An economic evaluation of the Oak Creek Range Management Area, Utah. General Technical Report INT-224. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 14 p.

An economic analysis on the Oak Creek Range Improvement Project was conducted under the Intermountain Region's Range Validation Program of the Forest Service, U.S. Department of Agriculture. The analysis provided information about the overall effectiveness of range improvement practices within pinyon-juniper ecosystems. The revegetation, fencing, and water development resulted in benefits to local ranchers and communities, but these estimated benefits were exceeded by the costs of the project.

KEYWORDS: economic evaluation, range management, benefit-cost analysis, cost effectiveness

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Forest Service

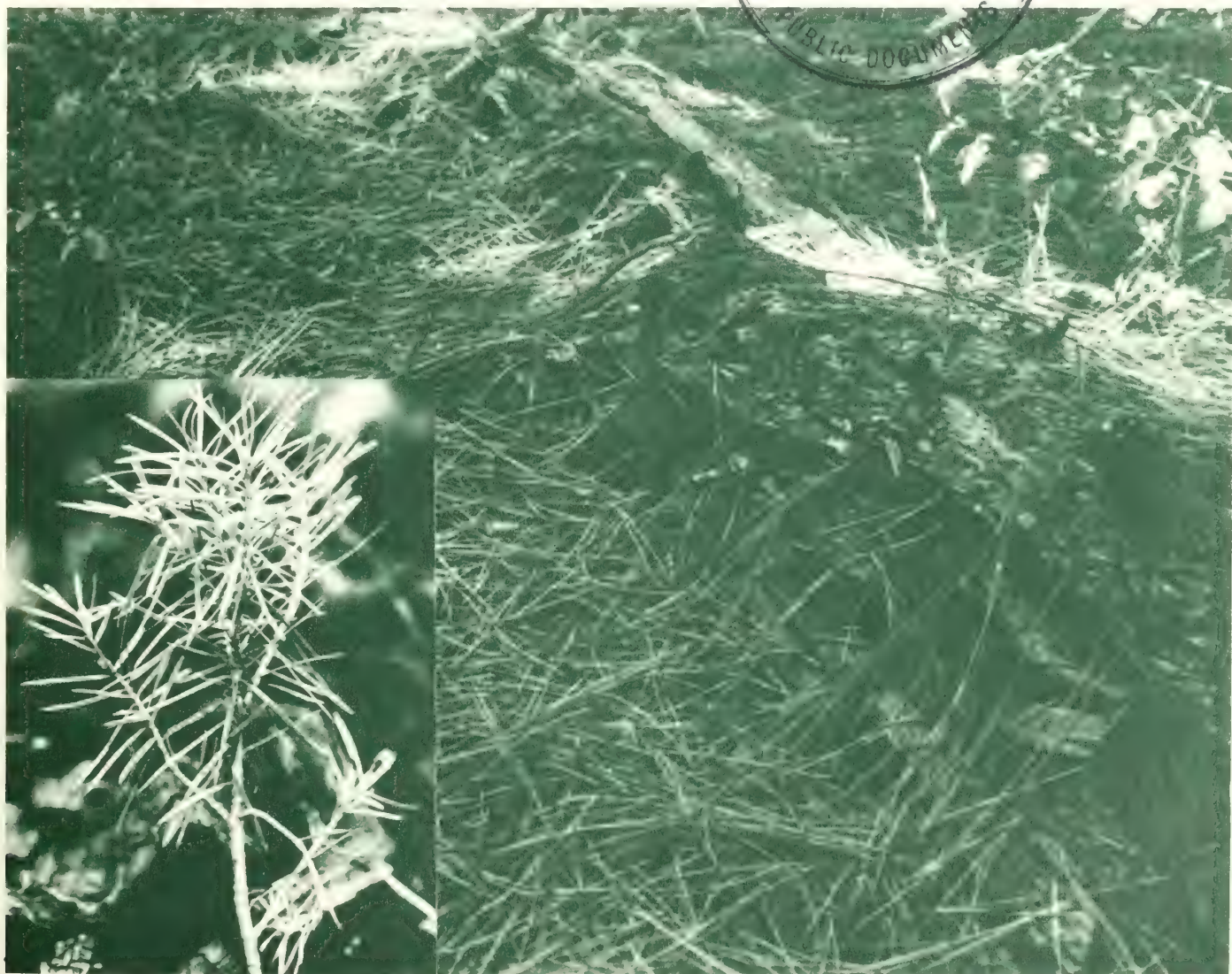
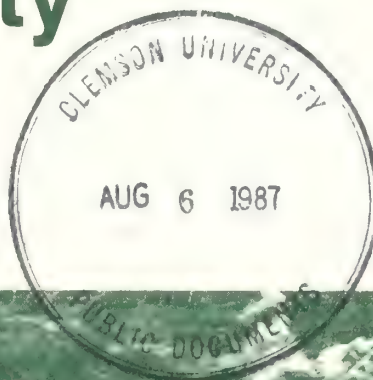
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General Technical
Report INT-225



Decaying Organic Materials and Soil Quality in the Inland Northwest: A Management Opportunity

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RESEARCH SUMMARY

Organic debris, including wood residues, provides parent materials for development and function of organic mantles on forest soils. Along with providing a storehouse of nutrients and moisture, organic materials provide either the environment or the energy source for microorganisms critical to both the nutritional quality of forest soils and the ability of conifers to extract nutrients and moisture from the soil. The role and relative importance of specific organic components can vary substantially with site and conifer species. Age of the trees appears to have less of an effect on importance of organic matter than site or species. Of the many organic materials incorporated in a forest soil, the woody component is in many ways the most important. To protect productive potential of forest soils, a continuous supply of organic materials must be provided, particularly in harsh environments. In case of excess losses of the organic mantle, complete recovery of the site may require several hundred years, even with proper management.

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INTRODUCTION

As practicing biologists, forest managers intuitively recognize that the organic forest floor, including decaying tree boles, has specific functions in forest ecosystems. Nearly all management operations have the potential to alter soil organic depositions and underlying mineral horizons. Some operations can cause considerable disruption to surface soil horizons. Site preparation procedures prior to reforestation frequently cause considerable physical soil disturbance. There is potential for increased use of prescribed burning as a site preparation and fuel management system. Application of intensive utilization practices and their greater wood removal in some areas of the Inland West appears probable. Appropriate application of these techniques can minimize soil disturbance. Inappropriate actions will likely reduce site productivity.

Many forests in the Inland Northwest have been accumulating high fuel loadings since the advent of Euro-American settlement. The danger of catastrophic wildfires that destroy forest floor organic materials (OM) is increasing in these areas. Extensive stands of overcrowded and stagnated timber are common throughout the Inland West. Many of these stands are probably growing in fire-damaged soils.

We have been investigating the potential for fire and logging to alter the possible roles that various organic materials, including woody residues, have in forested ecosystems. Our studies show that quantities of OM and their distribution, especially decaying wood and humus, have integral and sometimes critical roles to play in supporting the growth of forest trees. This report is a summary of this research and our assessment of how current forest practices are likely to impact future forest productivity in the Inland Northwest. We discuss a wide range of forest cover types, from warm, dry ponderosa pine (*Pinus ponderosa* Laws.) to cool, moist subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.).

For development and presentation of our results, concepts, and recommendations, we have emphasized measurements, or estimates based on measurements, taken from forest stands representative of commercial forests in the Inland Northwest. Literature citations are used only to

support specific points required to develop the concepts presented. Because of space limitations and difficulty of extrapolating from nonregional data, where possible we have emphasized literature based on research originating in the Inland Northwest.

Characteristics typifying the region discussed are a climate transitional between northern Pacific and continental United States with wet, cloudy winters and dry, sunny summers. Soils have moderate to low productivity potential (Pfister and others 1977), tend to be nitrogen limited, and usually have shallow organic mantles (Clayton and Kennedy 1985; Jurgensen and others 1979).

SOIL MICROBIAL FRAMEWORK

The chemical energy bound in soil organic matter and tree residues fuels important microbiological activities. Many microbes function as nutrient and OM (carbon) recycling agents. These microbes release or mineralize nutrients contained in plant remains, create many types of decay products (for example, brown, white, cubical, and stringy rots), capture and retain nutrients that might otherwise be leached from the root zone (Vitousek and others 1982), and form many of the chemical and physical components (for example, soil humus and organic cation exchange sites) responsible for maintenance of structure and fertility of forest soils. The wood decay fungi are perhaps the most important of these microbes because of the additional role rotted wood plays in sustaining certain conifer rooting, nitrogen (N) input, and nutrient storage capabilities.

Decay fungi have three major roles in the forest soil development process: (1) to break down plant residues and recycle the carbon (fig. 1A to C); (2) to release mineral nutrients in plants for use by other organisms (fig. 2A and B); and (3) to produce the physical character of the soil organic matrix (fig. 1C). In fulfilling these roles, low molecular weight carbon compounds are released and substantial volumes of OM, including decayed wood (fig. 3A and B), are deposited on and in the forest soil (fig. 4A and B). The carbon compounds are metabolized by various groups of soil microorganisms active in nutrient cycling, including the nonsymbiotic (NS) nitrogen-fixing bacteria.



Figure 1—(A) Natural forest residues are important parent materials that decay in place (B) to form deposits (up to 15 percent of surface soil volume) of decayed wood (C) in forest soils.

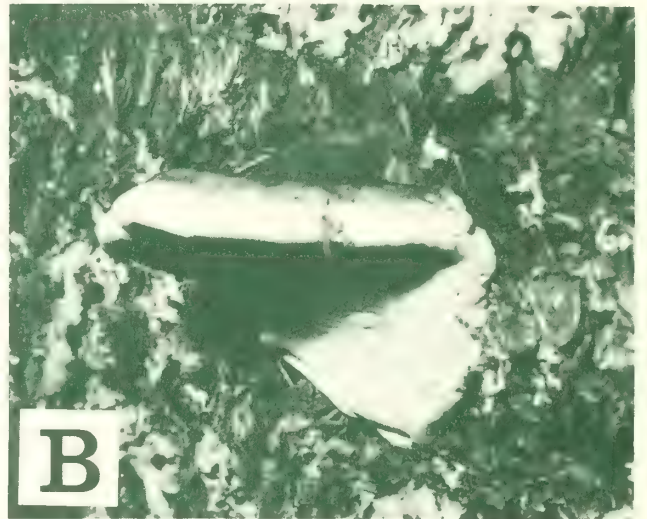


Figure 2—(A) *Phellinus pini* (Thore ex Fr.) Lloyd, an important heart rot fungus of living trees that produces rot columns inhabited by active populations of nonsymbiotic N-fixing bacteria; (B) *Fomitopsis pinicola* (Swartz ex Fr.) Karst., an important slash decay fungus that produces a brown, cubicle rot product that supports highly active populations of nonsymbiotic N-fixing bacteria.

The decayed soil wood forms long-lasting, high moisture microsites (Larsen and others 1980; Place 1950) important as an environment for NS-N fixation and for symbiotic ectomycorrhizal associations between certain fungi and conifer feeder roots (Harvey 1982; Jurgensen and others 1979).

Because forest soils of the Inland Northwest are frequently N limited (Pregitzer 1984) potential natural sources of N accretion in soils are important for continued productivity. There are only three natural sources: (1) precipitation, or N fixed by electrical discharge (lightning) and N in dust particles, pollen, or air pollutants; (2) symbiotic N fixation by legumes and other nodulated plants (for example, *Alnus*, *Ceanothus*, *Lupinus*) containing sym-



Figure 3—(A) Brown, cubicle, decayed wood frequently occurs as substantial deposits on and in forest soils; these deposits persist (at least 550 years) long after any resemblance to a decayed log remains; (B) Even in early stages of decay, the brown cubicle nature of the decay product produced by certain fungi (for example, *F. pinicola*) is evident; note active fungal growth that represents the early stage of fruiting body formation.

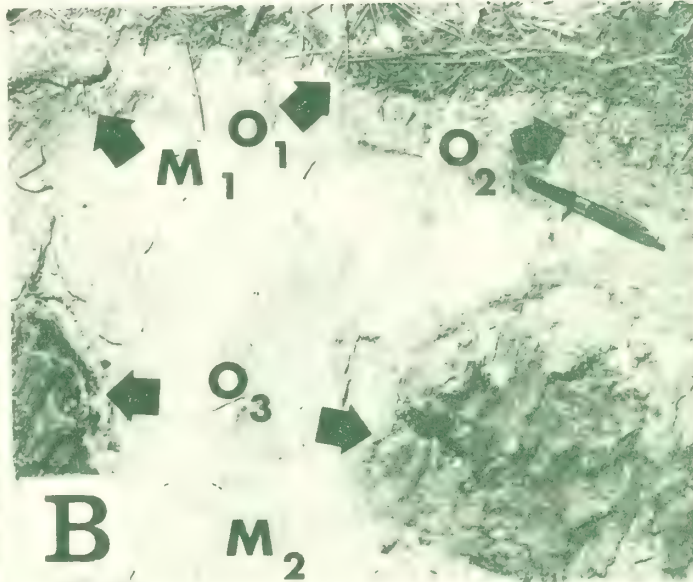
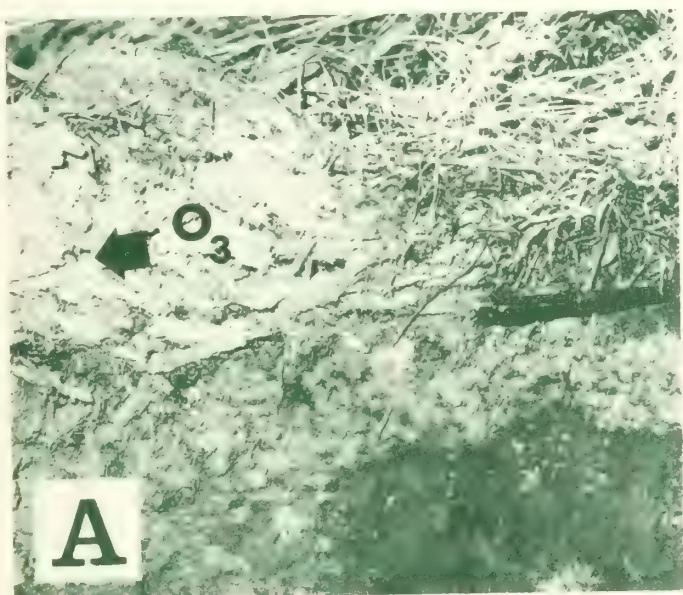


Figure 4—(A) Soil profile (cross-section) containing a surface deposit (old log) of decayed wood partially incorporated into the upper horizons; (B) profile containing deep deposits (old roots) of decayed wood in soil. Note that the primary organic-containing horizons—layers of litter (O_1), humus (O_2), decayed wood (O_3), and surface mineral base (M_1), with the exception of old roots—occur above the pen in both photos. These shallow horizons represent 60 to 70 percent of the stored N in these soils (table 2). Thus, the 5-30 cm mineral horizon (M_2) contains a relatively small portion of the stand N.

biotic associations with N-fixing bacteria (Gordon and others 1979); and (3) nonsymbiotic N fixation by free-living, N-fixing bacteria that occur in soil and plant residues (Jurgensen and others 1979). The energy source for N fixation by symbiotic bacteria is provided by the living host plant. Nonsymbiotic bacteria get their energy from the simple carbon compounds released from OM and plant

residues by decay fungi (fig. 2A and B, fig. 3B). Although symbiotic N-fixation is the most efficient process, most ecosystems in the Inland Northwest have few nodulated species, particularly in the absence of historical fire (Gruell 1986), and therefore, the ecosystems rely primarily on nonsymbiotic sources of nitrogen (Jurgensen and others 1979).

The symbiotic association between conifer roots and fungi (ectomycorrhizae) is another important microbial activity for functioning forest ecosystems (Robinson 1967; St. John and Coleman 1983). Again, as was the case for symbiotic N fixers, this is an invasive association wherein the energy for microbial metabolism is contributed by the host plant (Hacskeylo 1973). In this case, the fungus is not involved in fixing N. Rather, it improves the ability of tree root systems to extract fixed N and water from the soil (Bowen and Smith 1981; Harley 1978). This association is also an effective aid for acquiring other nutrients, particularly phosphorus (Harley 1978; Morrison 1962). Thus, it is an important aid to tree growth in infertile soils. Both mycorrhizal and N-fixing associations form varied but distinctive structures on root systems (short roots and nodules, respectively) and make a direct contribution to the growth of the host plant (Gordon and others 1979; Trappe and Strand 1969).

Another microbial action of varying importance is the association among conifers and aggressive root and stem decay fungi that cause disease. Although the products of the disease process, in the form of decayed and decaying wood, form an environment conducive to NS-N-fixing organisms (fig. 2A) (Harvey and others in preparation), the cost in tree mortality and wood loss can be high. In this case, the disease fungi contribute directly to reduced performance of the individual host even though, in the long term, the nitrogen fixed is utilized by the next generation. In most cases, the potential for nitrogen input from diseased tissue appears relatively small.

THE NATURE OF THE SOIL

Forest soils of the Inland Northwest are usually Inceptisols. However, they contain five easily recognized components: (1) the litter layer, consisting of recognizable plant debris (leaves, etc., designated as the O_1 or O_i horizon); (2) the humus layer, consisting of dark, extensively decayed and disintegrated organic detritus (designated as the O_2 , or O_e , and O_a horizon)—forest floor is a term that refers to the combined humus and litter layers; (3) decayed wood, consisting of the usually brown colored crumbly mass of residual lignin left from decaying woody material that has been incorporated into the soil; (4) charcoal, or extensively charred wood mixed in soil as a result of historical fire activity; and (5) the mineral soil material. We usually separate the mineral soil into two strata based on OM content. The surface 5 cm of mineral soil is a transition layer that occurs immediately below the humus layer. It tends to have incorporated humic materials. The mineral soil below this surface layer has a low organic content, normally less than 5 percent, and a higher bulk density (fig. 4A and B).

Each of the soil horizons or soil components listed above supports specific microorganisms and rooting activities that usually improve the soil quality as a medium for tree growth. Each component has a unique chemical and physical character based on its organic content, physical layering, and nature of underlying parent materials. In our discussion, we will concentrate on the surface 30 cm, particularly the organic mantle, because most conifer roots are there (Kimmins and Hawkes 1978), and it is easily

disrupted or destroyed by forest management activities. If extensively disrupted, removed, or destroyed, drastic reductions of growth, perhaps to the point of deforestation, can result (Hayes 1970; Weber and others 1984). However, deeper soil horizons may also be important to tree growth, especially on dry, sandy soils (Van Rees and Comerford 1986).

BASIC FUNCTIONS OF THE SOIL ORGANIC MANTLE

The organic and mineral components that make up the soil mantle have a variety of physical and chemical characteristics important to biological processes (Larsen and others 1980). Dead plant bodies tie up substantial quantities of nutrients, tend to retain large quantities of moisture, and can restrict air, sunlight, and large animal movement. Chemical energy bound in plant carbon compounds fuels important microbiological activities that represent major factors in the physical development of soils, in plant nutrition, and in the spread of insects and diseases (USDA FS 1980).

Organic detritus buried in the soil profile improves aeration, increases structure, infiltration, percolation, and retention of moisture, and protects the soil from compaction (Lull 1959). Accumulated surface debris and woody residues represent potential fuel for wildfire, an important though sometimes problematical force in the development of Inland Northwest forests and the soils in which they grow (Habeck and Mutch 1973; Harvey and others 1979b). As residues decay they become incorporated into the soil and form an organic reserve (figs. 1C, 3A, and 4A and B). If decay (microbial oxidation) is slow and residue accumulation rapid, fire frequently intervenes. This is usually the case in the Intermountain West (Olson 1963). However, aggressive fire control is moderating recent fire cycles. If wood accumulation is excessive, burn temperatures may be high and organic removal (physical oxidation) excessive. The interactive roles for fire and decay in development of forest stands and soils can be important to site productivity (Harvey and others 1979b).

The amount of OM in Inland Northwest forest soils is usually low. Organic matter makes up less than 15 percent (volume) of the top 30 cm (feeder root zone) of these soils (Harvey and others 1976). As we will demonstrate, this 15 percent normally has the highest concentrations of nutrients, especially nitrogen, has substantial moisture-holding ability and cation exchange capacity (CEC), and supports most of the N-fixing activities and important symbiotic associations (ectomycorrhizae) that contribute directly to tree growth potential.

FOREST PRODUCTIVITY: THE ROLE FOR ORGANIC MATTER BEFORE DISTURBANCE

Perhaps the best way to examine importance of the organic mantle to forest productivity is to catalog organic reserves, examine their nature, and calculate their relative contributions to productivity potential. To do this we will examine three old-growth stands from western Montana

(Harvey and others 1979a) that represent the range of temperature-moisture conditions typical of commercial forests in the Northern Rocky Mountains. We will also examine, in lesser detail, old-growth stands typical of forests in northern Idaho and eastern Washington and second-growth stands in western Montana. Old-growth stands (150 to 250 years) subject to natural fire are useful examples because they represent the culmination of interactions between forest, climate, and soil development processes indicative of a long-term balance between productivity and stability. As such, old-growth stands provide a model with which we can compare ecologically similar, but disturbed systems, to determine if disturbance-related nutrient and OM losses are likely significant to growth potential, and how long reconstitution (repair) may take (Clayton and Kennedy 1985).

Most stands reviewed here have been discussed in detail elsewhere (Harvey and others 1981a, 1981b, 1979b; Jurgensen and others 1984; Larsen and others 1978) or are referenced with respect to appropriate habitat type or habitat series for which extensive vegetative descriptions are available (Daubenmire and Daubenmire 1968; Pfister and others 1977). Therefore, we will not attempt to further describe our model stands here.

Nutrient Distribution

Because most forest stands and soils of the Inland Northwest tend to be N limited, sources for N and N reserves (stored N or N pool) can limit productivity. Table 1 shows the organic components contained in the three

old-growth Northern Rocky Mountain forests, and the relative rates, amounts, and proportions of nonsymbiotic N fixation associated with them. Sound stem wood and foliage are not considered until the recycling (decay) process begins with deposition on the forest floor. Table 2 shows the total and proportional distribution of nitrogen stored in these organic components.

It is apparent that decaying on-site residues and decayed wood in soil are particularly important as sources for nitrogen input and storage. The proportional distribution of these important N properties among the organic components subject to loss by displacement, removal, or burning indicates that most N cycling in forest soils is directly associated with surface organic materials (fig. 4A and B). Thus, organic reserves are critical to the N-based productivity of these sites, and they are highly vulnerable to potential loss (tables 1 and 2).

This is not all of the story. How N and other nutrients are distributed and exchanged within the soil and between the soil and aboveground components of a forest stand can also alter productivity (Meier and others 1985; Swank and Waide 1980; Vitousek and others 1982). For example, cold ecosystems, particularly cold-wet ecosystems, tend to accumulate N in organic components, sometimes to the detriment of productivity (low decay rate combined with long fire intervals) (Keeney 1980). However, we will emphasize N input (primarily fixation) and N storage in the soil and residue.

As with nitrogen, phosphorus is also concentrated in OM (table 3). However, phosphate is much less frequently in short supply and less subject to fire-induced losses than N.

Table 1—Estimated organic materials (OM) reserves and nonsymbiotic nitrogen fixation rates and amounts associated with residues and soil components of three old-growth forests representative of the Northern Rocky Mountains

Component	Organic content	N-fixation rate ²	N-fixation amount	Percent of site total	Percent ¹ N fixation vulnerable
	mg/lha	g ⁻⁹ /g/day	g/hal yr		
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> ³ (Douglas-fir/ninebark)					59
Residue	45.1	18.7	160	21	
Soil wood	37.0	9.0	94	12	
Forest floor	26.3	11.1	93	12	
Mineral, 0-5 cm	29.1	.8	106	14	
Mineral, 5-30 cm ⁴	73.4	.6	320	41	
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> (subalpine fir/clintonia)					76
Residue	145.7	21.5	515	40	
Soil wood	35.9	16.9	161	13	
Forest floor	36.0	19.5	197	15	
Mineral, 0-5 cm	26.1	1.0	106	8	
Mineral, 5-30 cm	85.8	.7	305	24	
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> (western hemlock/clintonia)					67
Residue	83.2	15.9	230	26	
Soil wood	50.5	9.3	120	14	
Forest floor	49.7	10.2	125	14	
Mineral, 0-5 cm	29.3	.9	117	13	
Mineral, 5-30 cm	68.6	.7	290	33	

¹Amount of nitrogen-fixing capacity associated with surface OM depth subject to displacement or volatilization in harvesting and site-preparation operations.

²Theoretical conversion ratio of acetylene reduction to nitrogen fixation 3:1.

³Habitat type (Pfister and others 1977).

⁴Mineral soil to 30 cm total depth.

Table 2—Estimated nitrogen reserves associated with residues and soil components of three old-growth forests representative of the Northern Rocky Mountains

Component	Organic content	Nitrogen	Total pool	Percent of total	Percent ¹ N storage vulnerable
	mg/ha	Percent	kg/ha/N		
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> ² (Douglas-fir/ninebark)					56
Residue	45.1	0.15	68	3	
Soil wood	37.0	.72	419	16	
Forest floor	26.3	.84	438	17	
Mineral, 0-5 cm	29.1	.07	543	21	
Mineral, 5-30 cm ³	73.4	.04	1,162	44	
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> (subalpine fir/clintonia)					62
Residue	145.7	.15	219	9	
Soil wood	35.9	.65	344	14	
Forest floor	36.0	.85	570	24	
Mineral, 0-5 cm	26.1	.06	343	14	
Mineral, 5-30 cm	85.8	.04	908	38	
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> (western hemlock/clintonia)					64
Residue	83.2	.15	125	5	
Soil wood	50.5	.52	341	14	
Forest floor	49.7	.96	787	33	
Mineral, 0-5 cm	29.3	.04	264	11	
Mineral, 5-30 cm	68.6	.04	867	36	

¹Amount of nitrogen pool associated with surface organic materials (above M₂ horizon) subject to displacement or volatilization in harvesting and site preparation operations.

²Habitat type (Pfister and others 1977).

³Mineral soil to 30 cm total depth, the feeder root zone.

Table 3—A summary of chemical and physical properties of soils from two old-growth forests representative of the Northern Rocky Mountains

Physical properties														
Stand	Texture			Classi- fication	Field capacity	Wilting point	Organic materials	Cation exchange capacity	Chemical properties ¹					
	Sand	Silt	Clay						pH	N	P	Ca	Mg	K
	- - - Percent - - -								Percent			meq/100 g		
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> ² (Douglas-fir/ninebark)														
Litter	—	—	—		—	—	69.0	—	5.4	1.08	0.26	2.19	0.14	0.12
Humus	—	—	—		101.2	71.5	46.9	—	5.9	.79	.24	1.39	.16	.12
Soil wood	—	—	—		198.7	128.0	63.4	—	4.9	.72	.14	1.04	.09	.07
												--- meq/100 g ---		
Mineral-trans	42	45	13	loam	27.8	8.7	8.6	35.0	5.5	.16	.02	17.8	1.7	0.6
Mineral-30 cm	46	40	14	loam	30.8	5.7	5.1	18.7	5.7	.08	.01	10.6	1.4	.4
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> (western hemlock/clintonia)														
												---- Percent ----		
Litter	—	—	—	—	—	—	78.5	—	5.1	.91	.29	1.42	.10	0.11
Humus	—	—	—	—	138.4	120.6	56.6	—	4.7	.97	.29	1.15	.13	.11
Soil wood	—	—	—	—	179.5	137.1	70.3	—	4.5	.52	.11	.84	.07	.11
												--- meq/100 g ---		
Mineral-trans	47	40	13	loam	26.3	8.6	7.8	15.1	5.8	.07	.02	11.5	1.0	0.3
Mineral-30 cm	47	39	14	loam	29.3	9.6	5.5	12.6	6.3	.07	.01	8.1	1.0	.3

¹Organic samples are expressed as total amounts. Mineral samples are expressed as: available P, Ca, Mg, and K as exchangeable.

²Habitat type (Pfister and others 1977).

Phosphorus is a part of parent minerals and not easily volatilized. It can, however, be tied up and rendered unavailable in certain volcanic ash soils. Other nutrients are more evenly distributed in the soil profile and even less subject to loss. Sulfur, like nitrogen, can be volatilized, but sulfur is a component of soil minerals and an im-

portant air pollutant (as opposed to biologically fixed N) not often in short supply nor subject to heavy loss, as is the case for N.

It should be noted that fire-caused losses of N can be overestimated. If calculations are based only on losses of specific organic components, estimates may be high.

However, if the entire soil profile is considered, N levels may increase in deep soil horizons after a fire. Apparently the cool, moist, mineral soil can act as a condenser that captures a portion of the N volatilized from the forest floor (Mroz and others 1980). Nitrogen losses associated with a moderate prescribed burn (*Abies lasiocarpa*/*Clintonia uniflora* habitat type) after clearcutting in western Montana were estimated at only 6 percent of the total in the surface 30 cm of soil (Jurgensen and others 1981). (A moderate fire is herein considered representative of flame lengths from 1 to 2 m, as described by Ryan and Noste (1985), with the temperature at the mineral soil surface not exceeding 150 °C.) However, these losses would likely be much larger from a wildfire during extremely dry conditions, when the upper mineral layer is dry and easily heated (Grier 1975).

Rooting Activity

It is appropriate now to examine distribution of the primary plant organs (feeder roots and ectomycorrhizal short roots) responsible for extracting nutrients from the soil system. Table 4 shows the distribution of ectomycorrhizal short roots among soil components from the same three stands used to evaluate nutrient distribution. As was the case with N, there is a disproportionate concentration of ectomycorrhizae in the organic components. Proximity

Table 4—Proportion of soil volume represented by various soil components and proportion of ectomycorrhizal root tips found in respective soil component¹

Soil component	Soil volume	Ectomycorrhizae distribution	Average number of ectomycorrhizal tips
----- Percent -----			Tips/core
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> ² (Douglas-fir/ninebark)			
Litter	1	14	9
Decayed wood	7	33	20
Humus	11	30	19
Mineral soil	81	23	14
			62
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> (subalpine fir/clintonia)			
Litter	2	0	0
Decayed wood	13	19	19
Humus	12	74	74
Mineral soil	73	7	7
			100
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> (western hemlock/clintonia)			
Litter	4	6	34
Decayed wood	16	51	297
Humus	12	32	187
Mineral soil	68	11	62
			580

¹To 30 cm depth, that is, feeder root zone as determined by random soil core sampling, 50 cores per stand, from three old-growth stands (250 years) representative of the Northern Rocky Mountains.

²Habitat type (Pfister and others 1977).

Table 5—Proportional volume of soil components and proportion of 100 natural seedlings (each site) with more than half of their root system in respective soil component, from three old-growth stands representative of the Northern Rocky Mountains

Soil component	Soil component volume ¹	Root system distribution ²
----- Percent -----		
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> ³ (Douglas-fir/ninebark)		
Moss ⁴	—	0
Soil wood	7	71
Humus	11	25
Mineral soil	82	4
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> (subalpine fir/clintonia)		
Moss	—	0
Soil wood	14	46
Humus	14	49
Mineral soil	72	5
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> (western hemlock/clintonia)		
Moss	—	8
Soil wood	17	39
Humus	12	48
Mineral soil	71	5

¹Includes soil depth to 30 cm, primary feeder root zone; seedling root systems averaged approximately 14 cm depth.

²Seedling included as representing a soil component if more than 50 percent of its root system was in that component. Seedling species primarily Douglas-fir, subalpine fir, western hemlock, and western redcedar.

³Habitat type (Pfister and others 1977).

⁴Data not available, estimated less than 1 percent.

of mycorrhizae to nutrient supplies likely enhances uptake efficiency (St. John and Coleman 1983). Also, fine root and ectomycorrhizal turnover contributes directly to OM and nutrient cycling and accumulation in upper soil horizons (Fogel and Hunt 1983; Vogt and others 1980).

In table 5 we show data from randomly selected, successful natural seedlings, again under these same stands. These seedlings were sampled by digging them up, following their root systems, and recording ectomycorrhizal distribution among the various soil components (Harvey and others 1987). Results were almost identical to the distribution of ectomycorrhizae on root systems of the older trees. Thus, both the occurrence of ectomycorrhizal activities and the distribution of feeder roots from conifers, young or old, are concentrated in soil OM. So both the nutrients and the means of acquiring them are highly dependent on the presence of organic components in old-growth systems.

Changing Sites

There is an obvious effect of site on the role of OM where there is a history of or high risk for insect, disease, or animal predation problems. Tree litter has the potential to increase damage caused by these organisms and to contribute to further spread of the problem (Fellin 1980). Even if problem organisms are not causing damage, litter may still contribute to the development of damage by providing an environment that attracts insects or animals, or

that supplies inoculum sources for pathogenic fungi (Fellin 1980; Nelson and Harvey 1974; Ream and Gruell 1980).

Although less conspicuous, the relative importance of a soil organic mantle in supporting beneficial microorganisms on different sites is also subject to change. This is the case for both NS-N fixation and ectomycorrhizal activities. For example, table 1 shows the rate of N input (fixation) potential is less on the dry site (*Pseudotsuga menziesii*/*Physocarpus malvaceus*) than on more moderate sites (*Abies lasiocarpa*/*Clintonia uniflora* and *Tsuga heterophylla*/*Clintonia uniflora*). Similarly, the numbers of ectomycorrhizal roots in the soil reflect relative harshness and productivity potential (table 4). Also, if we specifically examine the role of soil wood in supporting root development, we find that the relative importance of this component to dry sites can be much greater than to moist sites (table 5). Thus, there is the potential for the soil OM to be most important to sites on which it is the most difficult to produce (low productivity sites).

FOREST PRODUCTIVITY: THE ROLE FOR ORGANIC MATTER AFTER DISTURBANCE

Although the role for soil OM in forest productivity after disturbance is similar to before, several minor alterations can occur. These changes are mediated primarily through rapid release of nutrients from organic horizons caused by stand opening (fertilization effect), changes of stand species composition, displacement or loss of OM potential needed for regeneration or developing young stands, and the effects of competing vegetation.

The data in this section come largely from studies of subalpine fir and Douglas-fir habitat series typical of northern Idaho and western Montana.

The Fertilization Effect

Perhaps most obvious of postdisturbance changes is the resulting fertilization effect. When the stand is opened due to harvesting, fire, or wind, soil temperature and moisture levels increase (Hungerford 1980; Larsen and others 1980), resulting in acceleration of OM decomposition by microbes, or pyrolysis in the case of fire, which releases nutrients tied up in undecayed OM (Jurgensen and others 1979). This effect is shown in table 6 for mineral N and pH. All nutrient concentrations returned to preharvest levels within the second year after disturbance, except for pH, which remained high for at least 4 years after burning (Jurgensen and others 1981). Nutrient concentrations and distribution do not change radically unless disturbance is severe. In the case of severe disturbances, either fire (Niehoff 1985) or mechanical (Nielson-Gerhardt 1986) changes can be extreme. Obviously, large removals of nitrogen and significant losses of OM-derived cation exchange capacity are possible.

Changing Species Composition

Another potential concern after disturbance involves changes in species distribution; climax conifer species may be replaced by pioneer and seral species. Species suited for early ecosystem development may be better adapted to a low OM soil. Although this may well be the case, table 7 shows that young, disturbed stands utilize soil organic components as a substratum for supporting ectomycorrhizal activity much as older stands do. In the stands studied, the primary species are pioneer—western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Dougl.)—and the youngest stands, 12 and 16 years, were extremely low in organic reserves. In the case of the 12-year-old lodgepole pine stand, organic components made up only 5 percent of the feeder root zone, but still

Table 6—Microbial and chemical characteristics of a forest soil impacted by management activities. Measurements taken the spring following disturbance, a minimum of 50 random cores per treatment. All stands depicted represent comparable subalpine fir (*Abies lasiocarpa*/*Clintonia uniflora*)¹ forests representative of the Northern Rocky Mountains.

Soil or microbial character	Nature of stand				
	Undisturbed	Partial cut	Partial cut, broadcast burn	Clearcut	Clearcut, broadcast burn
Active ectomycorrhizae (No. tips/liter) (all soil components)	600	175	40	1	0
Nitrogen fixation rate (g/ha/day) (all soil components)	22	ND ²	ND	16	9
Ammonium nitrogen (μg/g) (humus only)	25	ND	ND	40	75
Nitrate nitrogen (μg/g) (humus only)	8	ND	ND	9	12
pH (humus only)	5.6	ND	ND	6.2	7.5 ³

¹Habitat type (Pfister and others 1977).
²Not determined.
³Acidity remained low for at least 4 years; other chemical characteristics returned to predisturbance levels by the end of the growing season.

Table 7—Proportion of soil¹ volume represented by various soil components and distribution of ectomycorrhizal root tips found in soil components²

Soil component	Soil volume	Distribution of ectomycorrhizae
----- Percent -----		
Intermediate-aged stand (52 yrs)—lodgepole pine		
Litter	3	10
Soil wood	4	57
Humus	11	15
Mineral soil	83	18
Young stand (16 yrs)—western larch		
Litter	3	1
Soil wood	5	8
Humus	5	23
Mineral soil	87	68
Young stand (12 yrs)—lodgepole pine		
Litter	2	0
Soil wood	1	40
Humus	2	36
Mineral soil	95	24

¹To 30 cm depth, the feeder root zone.

²A minimum of 50 random cores and 100 random seedlings per stand. From three disturbed stands representative of the subalpine fir/clintonia habitat type (Pfister and others 1977) of the Northern Rocky Mountains.

supported 76 percent of the ectomycorrhizal activity (table 7). The large relative contribution of OM, particularly soil wood, to support ectomycorrhizae on the lodgepole pine-dominated sites, and smaller contribution on the western larch site, may be indicative of a species effect.

Regeneration

To examine an earlier stage of postharvest forest development we used the results of a postlogging and burning regeneration study in the Crowsnest Forest of Canada, just north of Glacier National Park, MT (Day and Duffy 1963). Table 8 shows that organic soil components can act as valuable seedbeds in the Canadian Rockies. Although we normally expect mineral soils to provide superior seedbeds, this is not always the case (Haig and others 1941; Minore 1972). Day and Duffy indicated that lodgepole pine

Table 8—Seedbed composition and natural seedling distribution from logged-over stands in the Crowsnest Forest in Canada¹

Seedbed	Area	Seedling distribution
----- Percent -----		
Muck	— ²	9
Litter	11.8	9
Moss	6.3	24
Decayed wood	16.5	24
Humus	44.9	12
Mineral soil	20.4	22

¹Seedling species are Engelmann spruce, Douglas-fir, and lodgepole pine. Most stands represent subalpine fir habitat series. After Day and Duffy (1963).

²Data for area not available.

more frequently utilizes mineral seedbeds than do Engelmann spruce (*Picea engelmannii* [Parry ex Engelm.]) or Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), another indication of a species effect. However, in all of the instances referred to, the organic mantle continues to play an important role in both disturbed and regenerating forests.

Competition and Early Stand Development

At this point, discussion of interactions between conifers and nonconifers, as they may impact the relative ability of each to grow, is largely premature. However, it is interesting to speculate that destruction of soil organic reserves by repeated wildfires over the last 75 years may have contributed to the development of many aggressive shrubfields in northern Idaho. Repeated (often severe) wildfires were particularly common in the Northern Rocky Mountains early in this century (Wellner 1970).

Reforestation processes may require long-term reconstitution of organic horizons and nitrogen reserves for young conifers to be competitive with the other vegetation. A specific observation we have made regarding soil wood and competition is that, despite prolific rooting of conifers in this substratum, few roots of other plants are found. Thus, soil wood may provide a selective substratum for conifer roots. We have frequently noted selective occurrence of seedlings associated with deposits of decayed wood throughout the Inland Northwest, particularly on harsh sites (fig. 1C, fig. 5). Current research is emphasizing the interactive roles of soil components and site preparation as they affect reforestation.



Figure 5—Young Douglas-fir seedlings, and other conifers, are frequently observed in and associated with old logs and soil wood deposits.

THE MANAGEMENT OPPORTUNITY

Protection or enhancement of the forest soil's organic mantle, via manipulation of woody residues and other organic soil components, provides a major tool for impacting growth in forest ecosystems. In many ways manipulation of the organic constituents of soils is the only practical tool available for mitigating effects of harvesting systems that remove most of the standing crop or that cause extensive soil disturbance. Tree growth in Inland Northwest forest ecosystems can be dependent on the ability of a soil to retain moisture and to support N-fixing and ectomycorrhizal organisms. This ability, in turn, is largely dependent on the presence of an adequate organic base. Thus, large losses of OM from thin or infertile soils are likely to result in substantial losses of productivity. This leads to the other obvious questions: how much OM and of what kind do we need to protect the productivity of our forest soils?

How Much

There can be too much as well as too little OM on the soil surface. Too much may lead to excess fuel loading and high fire risks that, in turn, may lead to too little. All organic soil constituents decay, and presumably more decay increases the associated N input and potential for productivity. Because part of that productivity (the high-risk fuel component) may carry great risk, we must stay within fuel management guidelines if we are to deliberately enhance the organic mantle. Thus, possible management of N input, via N-fixation through residue manipulation, is at least limited by risk of fire.

The other major beneficial microbial activity, ectomycorrhizal infection, particularly in infertile soils, can also be useful in establishing management targets for adjusting OM composition of forest soils. By dividing soil samples containing ectomycorrhizae according to the quantity of OM they contain, and then relating organic percentage to ectomycorrhizal activities, we were able to provide estimates for the question of quantity of organics desired. Our initial recommendation of 22.4 metric tons/ha was based on a large data set from the three western Montana sites (Harvey and others 1981a).

Let's reexamine how this recommendation was derived and see how well it holds for two productive northern Idaho sites and a moisture-limited, harsh site from eastern Washington. Table 9 shows the relationship between organic percentage and ectomycorrhizal activity. Optimal activity on all six sites occurred between 15 and 45 percent OM content. In no case were additional benefits realized from organic levels in excess of 45 percent of the surface 30 cm of soil. On the other hand, there were reduced activities, in all cases, when organic volumes in the surface 30 cm of soil were less than 15 percent.

By conservatively assuming that a substantial portion of the soil OM required to support future stand growth will be derived, at least indirectly, from woody residues, we can calculate a theoretical residue loading based on the 31 to 45 percent figure and see if the result is reasonable and meets potential fuel loading limits. By assuming a 40 percent loss of volume from the time a log becomes fresh

residue to when it begins functioning as a soil component (based on field observations), and converting the percentage figure to volume, then to weight, we find a soil minimum of 22.4 metric tons/ha. Add 12 metric tons/ha for suspended residues in an advanced state of decay but not yet incorporated in the soil, and we have a recommended 22 to 36 t/ha. This figure is well within fuel management guidelines. Due to the general infertility of Inland Northwestern forest soils, we would not generally recommend removing foliage or small twigs (because of their relatively high nutrient content) from most forested sites (Stark 1980). This would be particularly true of the cold, infertile ecosystems characteristic of the eastern slopes of the Central and Northern Rocky Mountains (Harvey and others in press; Yavitt 1984).

The general recommendation cited above seems appropriate for all six sites shown in table 9, but with reservations for the extreme dry and moist ends of the moisture gradient represented. On the moist end the ability of OM to absorb and hold water may create a situation of excess moisture and lower soil temperatures where deposits are heavy. Therefore, because these sites are productive and should replace lost organic horizons quickly, we do not consider them sensitive. On the other hand, replacement of OM on dry sites will take place slowly, so they can be considered extremely sensitive to loss of organic soil components.

The ponderosa pine site requires further clarification. High levels of OM on this site were not effective in supporting ectomycorrhizal roots, though high organic levels were effective on the dry Douglas-fir site. We interpret this as an indication moisture was so limiting on the

Table 9—Relationship of active ectomycorrhizal root tips (percentage of total) to soil organic matter content (50 random cores per site from undisturbed stands)

		Organic matter volume (percent)			
Location	Series ¹	0-15	16-30	31-45	>45
----- Percent -----					
Western Montana	Douglas-fir, series dominated by Douglas-fir	7	36	52	5
	Subalpine fir series, dominated by subalpine fir and spruce	12	58	27	3
	Western hemlock series, dominated by western hemlock	13	45	23	19
Northern Idaho	Western hemlock series, dominated by western redcedar ²	20	49	21	10
	Western hemlock series, dominated by western white pine	12	20	41	27
	Ponderosa pine series, dominated by ponderosa pine	38	44	18	— ³

¹Climax type as defined by Pfister and others (1977).

²Western redcedar is largely nonectomycorrhizal; mycorrhizae are from the hemlock component.

³Organic matter volumes this high did not occur.

ponderosa pine site that the organic mantle usually does not contain sufficient moisture during the growing season to maintain itself above the permanent wilting point. Thus, we do not think high levels of OM are a problem in this case, except as a potential wildfire hazard. Rather, the OM horizons have an extremely limited period (late spring) to be effective.

Although the above interpretations are derived primarily from old-growth models, it is worthy of note that distribution of ectomycorrhizal activity shows similar patterns in second-growth stands (table 7) and for natural regeneration (Harvey 1982; Harvey and others 1987; Vogt and others 1980). Thus, pioneer or seral species may do better than climax species in low soil OM situations, but we should expect their performance to improve in high OM soils.

What Kind

In the Inland Northwest, forest soils we examined have a ratio between soil humus and soil wood volume that is about equal—1:1 (see organic content in table 1). Both soil components contain substantial quantities of nutrients and both retain moisture well. Wood deposits tend to be large (remains of old logs and roots) so they are effective in moisture storage. Litter and humus, on the other hand, occur in shallow, sometimes discontinuous layers that dry quickly (fig. 4A and B). Each organic component also has unique characteristics with respect to nitrogen relationships. For example, decaying woody residues and decayed soil wood are more effective than other organic materials for supporting high levels of NS, N-fixing activities (table 1), and the forest floor has a greater role for retaining (storing) fixed nitrogen and adsorbing cations than do woody materials (table 2). A similar contrast occurs with ectomycorrhizal activities. In periods of adequate moisture, humus supports the highest levels of ectomycorrhizae but, during periods of drought, soil wood becomes the most active site (Harvey 1982; Harvey and others 1979a; Larsen and others 1982). Thus, we recommend that litter, humus, and woody materials all be carefully maintained in forest soils. This reemphasizes that smaller woody residues and foliage not be removed. They are converted to humus rapidly and contain relatively high quantities of nutrients.

Concerning the conversion of woody residue into the soil wood component, we must consider tree species distribution. We have identified the species of wood contained in the soil of four ecosystems of the Inland Northwest area. Table 10 shows the distributions of species of soil wood found on those sites. These wood identifications indicate that Douglas-fir, western larch, western white pine (*Pinus monticola* Dougl.), and lodgepole pine are the most effective species for producing highly persistent, brown rotted soil wood. Ponderosa pine is also effective (field observations) but did not occur on these sites. Other species, such as western redcedar (*Thuja plicata* Donn ex D. Don), grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.), subalpine fir, and Engelmann spruce, usually decay into white, stringy, fibrous materials that do not persist as distinct deposits. Thus, we would add to our residue requirement that, if possible, the 24 to 36 metric tons/ha be

Table 10—Species distribution of decayed wood in soils of four old-growth forests representative of the Northern Rocky Mountains¹

Habitat series ²	Total samples	Species ³						
		DF	WWP	WL	LPP	WH	SAF	ES
----- Percent -----								
Western Montana								
Douglas-fir	22	100	0	0	0	0	0	0
Subalpine fir	101	77	0	8	3	2	6	4
Western hemlock	16	63	0	0	6	19	6	6
Northern Idaho								
Western hemlock	153	45	49	16	1	4	1	2

¹Random samples. Number varies according to wood presence and sampling history.

²Climax type as described by Pfister and others (1977).

³Species codes are DF = Douglas-fir, WWP = western white pine, WL = western larch, LPP = lodgepole pine, WH = western hemlock, SAF = subalpine fir, and ES = Engelmann spruce.

of one of the more effective species—preferably Douglas-fir, but western white pine and western larch also appear acceptable.

How Long

What would happen if excessive site degradation, through loss of organic reserves, should occur? How long would it take for the ecosystem to rebuild its potential productive capacity? This has been a difficult question because soil development is a dynamic process in which nutrients and carbon circulate between the aboveground and belowground components and within the soil system itself. Methods for estimating time for organic horizon accumulation are crude. However, we used three systems for calculating OM (wood) cycling time, and all produced similar results.

The most straightforward approach is to measure the age of decaying wood by C¹⁴ analysis. The most likely source of error with this method is an underestimation of age from contamination of the sample with organic materials of recent origin. Table 11 shows that the C¹⁴ age of soil wood varies from 246 to 473 years, depending on habitat type (Harvey and others 1981b). Another source of error with this method is the possibility that soil wood will persist longer on gentle slopes due to lack of downslope soil movement and resultant breakup of wood deposits. This is probably the reason for older wood on the hemlock/clintonia habitat type.

Another means of calculating site recovery time is to measure N content in the wood components and divide the total by the indigenous N fixation rate. Residue N recovery time (not yet buried in the soil) was similar to the C¹⁴ soil wood age estimate using this calculation. Soil wood was not useful because of N import from other soil components. Recovery times varied from 425 to 543 years (table 11). This method does not include time required to grow the residue, but it also does not account for N in the stem at the time of death, which should compensate for the age factor.

Table 11—Estimated recovery times, assuming total removal of woody residues, from three old-growth forests representative of the Northern Rocky Mountains

Component	Total N associated with component	N-fixation rate associated with component	Recovery time ¹	C ¹⁴ age	Decay age ²
	kg/ha	g/ha/yr	----- Years -----		
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> ³ (Douglas-fir/ninebark)					
Residue	68	160	425	—	—
Soil wood	419	94	—	246 ± 90	192
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> (subalpine fir/clintonia)					
Residue	219	515	425	—	—
Soil wood	344	161	—	257 ± 90	274
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> (western hemlock/clintonia)					
Residue	125	230	543	—	—
Soil wood	341	120	—	473 ± 100	172

¹Assuming all input of nitrogen is based on internal activities.

²Estimated age based on productivity and decay rate (Harvey and others 1981b).

³Habitat type (Pfister and others 1977)

We also determined recovery time by calculating the ratio of total wood production potential (growth) to quantity of wood present in old-growth ecosystems (Harvey and others 1981b). This method provided estimates from 172 to 274 years (table 11). This method also underestimates age because growth projections did not account for standing decay.

In any case, if OM reserves (particularly woody components) are lost for any reason, it will take at least one rotation, perhaps two, to restore soil productivity potential based on that resource—that is, convert fresh wood residues (fig. 1A) into substantial decayed soil wood deposits (figs. 1C, 3A, and 4A and B).

Distribution Geometry

If we are to manage the soil organic mantle with systems that inevitably cause disturbance, we must consider the distribution as well as the potential loss of this resource. Initially, these materials must support a regenerating forest, that is, young trees with a limited ability to explore the soil system. Therefore, organic materials should be well distributed as well as conserved. Extensive heavy deposits or large areas with little or no OM are not desirable. We should create a mosaic of maximum possible diversity. This will create a situation where the precise balance of organic materials to mineral soil base required to support the desired site-species combination will be available on at least a small percentage of the acres treated, and it will be well distributed. When planting, seedlings should be placed near a source of organic material. Because of difficulty in getting seedling root to soil contact, they should not be placed directly in deep layers of OM.

Woody residues, as the source for decaying soil wood, should also be well scattered over the treated areas. Several logs per hectare could meet the minimum 22.4 metric tons/ha requirement, but it would not be sufficient. We also recommend, as noted earlier, that residues be of appropriate species (Douglas-fir, western larch, pines). Fresh residues should, if possible, be at least 10 to 15 cm

in diameter to provide for relatively deep soil wood deposits. Additionally, if the residues contain heartwood, they are more likely to produce brown cubicle rot, which is the most desirable form of soil wood. Distribution can be enhanced by using relatively short pieces if required. There are likely to be interactions between tree species requirement, climate, soil, and site preparation. This is an active and evolving area of research.

A PERSPECTIVE

Although the need to maintain minimum reserves of soil OM may constrain certain harvest management practices, it is likely to do so only in harsh, cool, or dry ecosystems, or in ecosystems with a severe fire or intensive logging history. Many Inland Northwest habitat types contain adequate organic reserves and are not considered highly sensitive to logging damage, and most of our current harvesting systems leave adequate residue. However, full tree harvesting should be used with caution; where possible, branch material should remain on site.

The most likely problem is with extensive site preparation, particularly piling or windrowing that displaces or destroys the forest floor over large areas. Similarly, scalping or furrowing displaces OM, but the area disturbed can be constrained. Such practices should be used with caution and for resolving specific problems (reduction of fuel or competition) on sites likely to be sensitive to OM loss. Where disturbance is necessary, it should be kept to a minimum. From a fire management perspective, extremely hot wildfires are also dangerous to site and soil productivity, particularly with sensitive (harsh) ecosystems. Also, prescribed burning should be carried out with care to assure that the 24-36 metric tons per hectare requirement for residual woody material is maintained after treatment.

Open-grown, short rotation forests (forests with low competition, maximum soil volume per tree, using pioneer or seral species and a potential for understory symbiotic N-fixers), with appropriate vegetation management seems a good biological approach to managing infertile, second-growth forests with low soil OM reserves. However, costs

of achieving these objectives on such sites are likely to be high. Returns from maintaining an adequate soil organic mantle can reduce these costs.

A recognition of the important role the organic soil mantle plays in forest soils will help alleviate and avoid site degradation caused by excessive disturbance. Guiding our actions with the use of a reasonable biological perspective represents an opportunity to maintain or even improve harvested sites and their soils as a firm foundation for future forestry.

REFERENCES

- Bowen, G. D.; Smith, S. E. The effects of mycorrhizas on nitrogen uptake by plants. In: Clark, F. E.; Rosswall, T., eds. *Terrestrial nitrogen cycles*. Ecological Bulletin (Stockholm). 33: 219-232; 1981.
- Clayton, J. L.; Kennedy, D. A. Nutrient losses from timber harvest in the Idaho batholith. *Soil Science Society of America Journal*. 49: 1041-1049; 1985.
- Daubenmire, R.; Daubenmire, J. B. Forest vegetation of eastern Washington and northern Idaho. *Technical Bulletin* 60. Pullman, WA: Washington Agricultural Experiment Station; 1968. 104 p.
- Day, R. J.; Duffy, P. J. Regeneration after logging in the Crowsnest Forest. Publication 1007. Calgary, AB: Canadian Department of Forestry; 1963. 31 p.
- Fellin, D. G. Relationships in harvesting and residue treatments to forest insect and disease activity. In: *Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: symposium proceedings*; 1979 September 11-13; Missoula, MT. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 335-416.
- Fogel, R.; Hunt, G. Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. *Canadian Journal of Forest Research*. 13: 219-232; 1983.
- Gordon, J. C.; Wheeler, C. T.; Perry, D. A. Symbiotic nitrogen fixation in the management of temperate forests: *Proceedings, National Science Foundation workshop*; 1979 April 2-5; Corvallis, OR. Corvallis, OR: Oregon State University; 1979. 401 p.
- Grier, C. C. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. *Canadian Journal of Forest Research*. 5: 599-607; 1975.
- Gruell, G. [Personal communication.] 1986 June 26. Intermountain Region, Forest Service, U.S. Department of Agriculture, Ogden, UT.
- Habeck, J. R.; Mutch, R. W. Fire dependent forests in the northern Rocky Mountains. *Quaternary Research*. 3: 408-424; 1973.
- Hackskaylo, E. Dependence of mycorrhizal fungi on hosts. *Bulletin of the Torrey Botanical Club*. 100: 217-223; 1973.
- Haig, I. T.; Harris, D. P.; Weidman, R. H. Natural regeneration in the western white pine type. *Technical Bulletin* 767. Washington, DC: U.S. Department of Agriculture; 1941. 99 p.
- Harley, J. L. Ectomycorrhizas as nutrient absorbing organs. In: *Proceedings: Royal Society of London Series B*. 103: 1-21; 1978.
- Harvey, A. E. The importance of residual organic debris in site preparation and amelioration for reforestation. In: *Site preparation and fuels management on steep terrain: symposium proceedings*; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension; 1982: 75-85.
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Residues, microbes, and soil management in cool, east slope Rocky Mountain lodgepole pine ecosystems. In: *Management of small stem stands of lodgepole pine: workshop proceedings*; 1986 June 30-July 2; Fairmont Hot Springs, MT. [In press].
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. Organic reserves: importance to ectomycorrhizae in forest soils in western Montana. *Forest Science*. 27: 442-445; 1981a.
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J.; Graham, R. T. Relationships among soil microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests in western Montana. *Canadian Journal of Forest Research*. 17: 58-62; 1987.
- Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J.; Jones, E. A. Nitrogen fixation associated with pathological decay of living north Idaho conifers. [In preparation].
- Harvey, A. E.; Larsen, M. J.; Jurgensen, M. F. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. *Forest Science*. 22: 393-398; 1976.
- Harvey, A. E.; Larsen, M. J.; Jurgensen, M. F. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types. *Forest Science*. 25: 350-360; 1979a.
- Harvey, A. E.; Larsen, M. J.; Jurgensen, M. F. Fire-decay: interactive roles regulating wood accumulation and soil development in the northern Rocky Mountains. Research Note INT-263. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979b. 4 p.
- Harvey, A. E.; Larsen, M. J.; Jurgensen, M. F. Rate of woody residue incorporation into northern Rocky Mountain forest soils. Research Paper INT-282. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981b. 5 p.
- Hayes, G. I. Impacts of fire on forested ecosystems. In: *The role of fire in the Intermountain West*. Missoula, MT: Intermountain Fire Research Council; 1970: 99-118.
- Hungerford, R. D. Microenvironmental response to harvesting and residue management. In: *Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: symposium proceedings*; 1979 September 11-13; Missoula, MT. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 37-74.
- Jurgensen, M. F.; Arno, S. R.; Harvey, A. E.; Larsen, M. J.; Pfister, R. D. Symbiotic and nonsymbiotic nitrogen fixation in Northern Rocky Mountain forest ecosystems. In: *Symbiotic nitrogen fixation in the management of temperate forests: proceedings, National Science Foundation workshop*; 1979 April 2-5; Corvallis, OR. Corvallis, OR: Oregon State University; 1979: 294-308.

- Jurgensen, M. F.; Harvey, A. E.; Larsen, M. J. Effects of prescribed fire on soil nitrogen levels in a cut-over Douglas-fir/western larch forest. Research Paper INT-275. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 6 p.
- Jurgensen, M. F.; Larsen, M. J.; Spano, S. D.; Harvey, A. E.; Gale, M. R. Nitrogen fixation associated with increased wood decay in Douglas-fir residue. *Forest Science*. 30: 1038-1044; 1984.
- Keeney, D. R. Prediction of soil nitrogen availability in forest ecosystems: a literature review. *Forest Science*. 26: 159-171; 1980.
- Kimmins, J. P.; Hawkes, B. C. Distribution and chemistry of fine roots in a white spruce-subalpine fir stand in British Columbia: implications for management. *Canadian Journal of Forest Research*. 8: 265-279; 1978.
- Larsen, M. J.; Harvey, A. E.; Jurgensen, M. F. Residue decay processes and associated environmental functions in Northern Rocky Mountain forests. In: Environmental consequences of timber harvesting in Rocky Mountain coniferous forests. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 157-174.
- Larsen, M. J.; Jurgensen, M. F.; Harvey, A. E. N₂ fixation associated with wood decayed by some common fungi in western Montana. *Canadian Journal of Forest Research*. 8: 341-345; 1978.
- Larsen, M. J.; Jurgensen, M. F.; Harvey, A. E. N₂ fixation in brown-rotted soil wood in an Intermountain cedar-hemlock ecosystem. *Forest Science*. 28: 292-296; 1982.
- Lull, H. W. Soil compaction on forest and rangelands. Miscellaneous Publication 768. Washington, DC: U.S. Department of Agriculture; 1959. 33 p.
- Meier, C. E.; Grier, C. C.; Cole, D. W. Below and aboveground N and P use by *Abies amabilis* stands. *Ecology*. 66: 1928-1942; 1985.
- Minore, D. Germination and early growth of coastal tree species on organic seedbeds. Research Paper PNW-135. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1972. 18 p.
- Morrison, T. M. Absorption of phosphorus from soils by mycorrhizal plants. *New Phytologist*. 61: 10-20; 1962.
- Mroz, G. D.; Jurgensen, M. F.; Harvey, A. E.; Larsen, M. J. Effects of fire on nitrogen in forest floor horizons. *Soil Science Society of America Journal*. 44: 395-400; 1980.
- Nelson, E. E.; Harvey, G. M. Residues and forest disease. In: Environmental effects of forest residues management in the Pacific Northwest—a state-of-knowledge compendium. General Technical Report PNW-24. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1974: S1-S9.
- Niehoff, G. J. Effects of clearcutting and varying severity of prescribed burning on levels of OM and the mineralization of ammonium nitrogen in the surface layer of forest soils. Moscow, ID: University of Idaho; 1985. 43 p. M.S. thesis.
- Nielson-Gerhardt, M. Effects of logging and mechanical site preparation on levels of mineralizable nitrogen and organic matter in forest soils. Moscow, ID: University of Idaho; 1986. 45 p. M.S. thesis.
- Olson, J. S. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*. 44: 321-322; 1963.
- Place, I. C. M. Comparative moisture regimes of humus and rotten wood. Silviculture Leaflet 37. Ottawa, ON: Canadian Department of Research and Development, Forestry Branch; 1950. 2 p.
- Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. Forest habitat types of Montana. General Technical Report INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 174 p.
- Pregitzer, Kurt S. Relating predicted fertilizer response to actual growth and site conditions. 1984 December. Final Report, Agreement 22-C-3-INT-39. On file at: RWU 4152 files, Forestry Sciences Laboratory, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Moscow, ID.
- Ream, C. H.; Gruell, G. E. Influences of harvesting and residue management on small mammals. In: Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: symposium proceedings; 1979 September 11-13; Missoula, MT. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 455-468.
- Robinson, R. K. Ecology of fungi. London: English University Press Ltd; 1967. 116 p.
- Ryan, K. C.; Noste, N. V. Evaluating prescribed fires. In: Lotan, J. E.; Kilgore, B. M.; Fischer, W. C.; Mutch, R. W., tech. coords. Symposium and workshop on wilderness fire: proceedings; 1985 November 15-18; Missoula, MT. General Technical Report INT-182. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1985: 230-259.
- St. John, T. V.; Coleman, D. C. The role of mycorrhizae in plant ecology. *Canadian Journal of Botany*. 61: 1005-1014; 1983.
- Stark, N. M. Impacts of utilization of nutrient cycling. In: Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: symposium proceedings; 1979 September 11-13; Missoula, MT. General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980: 123-136.
- Swank, W. T.; Waide, J. B. Interpretation of nutrient cycling research in a management context: evaluating potential effects of alternative management strategies on site productivity. In: Waring, R. H., ed. Forests: fresh perspectives from ecosystem analysis. Corvallis, OR: Oregon State University Press; 1980: 137-158.
- Trappe, J. M.; Strand, R. F. Mycorrhizal deficiency in a Douglas-fir region nursery. *Forest Science*. 15: 381-389; 1969.
- U.S. Department of Agriculture, Forest Service. Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: symposium proceedings.

- General Technical Report INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 526 p.
- Van Rees, K. C. J.; Comerford, N. B. Vertical root distribution and strontium uptake of a slash pine stand on a Florida Spodosol. *Soil Science Society of America Journal*. 50: 1042-1046; 1986.
- Vitousek, P. M.; Gosz, J. R.; Grier, C. C.; Melillo, J. M.; Reiners, W. A. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological Monographs*. 32: 155-177; 1982.
- Vogt, K. A.; Edmonds, R. L.; Grier, C. C.; Piper, S. R. Seasonal changes in mycorrhizal and fibrous-textured root biomass in 23- and 180-year-old Pacific silver fir stands in western Washington. *Canadian Journal of Forest Research*. 10: 523-529; 1980.
- Weber, M. G.; Methoen, J. F.; Van Wagner, C. E. The effect of forest floor manipulation on nitrogen status and tree growth in an eastern Ontario jack pine ecosystem. *Canadian Journal of Forest Research*. 15: 313-318; 1984.
- Wellner, C. A. Fire history in the Northern Rocky Mountains. In: *The role of fire in the Intermountain West: symposium proceedings*; 1970 October 23-29; Missoula, MT. Missoula, MT: Intermountain Fire Research Council; 1970: 42-69.
- Yavitt, J. B. Nitrogen in lodgepole pine forests in relation to decomposition and soil solution chemistry. Laramie, WY: University of Wyoming, Department of Botany; 1984. 228 p. Ph.D. thesis.



Harvey, Alan E.; Jurgensen, Martin F.; Larsen, Michael J.; Graham, Russell T. 1987. Decaying organic materials and soil quality in the Inland Northwest: a management opportunity. Gen. Tech. Rep. INT-225. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 15 p.

Organic debris, including wood residue, is important to the development and function of forest soil. Organic matter stores nutrients and moisture plus it provides important habitats for microbes beneficial to tree growth. To protect long-term forest soil productivity, organic horizons and their parent materials should be maintained.

KEYWORDS: forest soil, organic reserves, soil microbes, nitrogen fixation, ectomycorrhizae, harvesting and fire effects, regeneration, site preparation, soil management

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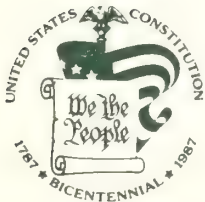
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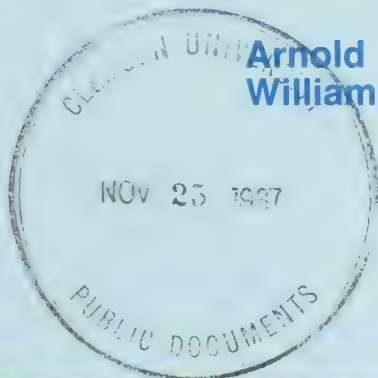
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Climate of the Deception Creek Experimental Forest, Northern Idaho

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RESEARCH SUMMARY

This report describes in detail the climate of Deception Creek Experimental Forest and adjacent area, located in the northern Idaho panhandle. Data are summarized from year-round climatological stations, fire-weather stations, and other sources. Primary observations within the experimental forest, taken at the headquarters, are limited to a 10-year period, 1936-45, but long-term averages have been derived employing standard methods. Indications of local site or topographic differences in temperature, relative humidity, and precipitation are given by station comparisons utilizing past data and also 1984-85 data acquired for fire research. The recent data include hourly measurements from a Remote Automatic Weather Station (RAWS).

Deception Creek's climate is distinguished by its heavy precipitation. The ravine-bottom headquarters location averages about 55 inches annually, compared with 26 to 42 inches at adjacent valley-bottom climatic stations. About 10 percent more precipitation occurs on a nearby ridgetop. Average precipitation of 1.00 inch during July, normally the driest month, is, however, close to that at the other climatic stations. Annual mean temperature at headquarters, 42 °F, is 5 to 6 °F lower than at neighboring Coeur d'Alene and Kellogg. Monthly normals range from 23 °F in January to 62 °F in July. Average maximum temperatures reach 81 °F in July, but this location is still subject to early-morning frost in summer.

An afternoon shading effect on temperature and relative humidity was found to occur at headquarters, particularly in late fire season. During a period of fair weather in late September and early October 1984, maximum temperatures at headquarters on 5 days were 10 to 16 °F lower than those at the RAWS site, on a north-facing slope 900 ft higher in elevation. By early September, minimum afternoon relative humidity at headquarters averages about 15 percent higher than at Fernan Ranger Station, Coeur d'Alene. By 4:30 p.m. (1630), P.s.t., at this time of year, the humidity difference between these two stations rises to about 30 percent. Afternoon data were therefore utilized from the former Magee Ranger Station, located northeast of Deception Creek, to more broadly represent a 3,000-ft elevation for interpolation purposes in certain graphs. From such a graph, the frequency of a midafternoon humidity value less than 30 percent at an open 4,000-ft slope location increases from about 6 percent of the days during May and early June to 50 percent in late July, falling to 10 percent in late September.

Data from Fernan Ranger Station, and from other fire-weather stations in the Northern Rocky Mountains, show large differences between pre-1974 and more recent (1974-84) averages of afternoon temperature and relative humidity—particularly in July and August. About one-half of these differences may represent a generally cooler, moister summertime pattern in recent years. The other half may be attributed to a 3-hour change in fire-weather observation time.

Cover photo: An early view of the Deception Creek Experimental Forest Headquarters site showing the location of the Headquarters weather station.
Forest Service photo by Charles A. Wellner, July 19, 1937.

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INTRODUCTION

This report is one of a series of climatological summaries for Northern Rocky Mountain forest areas. Previously published reports describe the climates of the Selway-Bitterroot Wilderness, the Priest River Experimental Forest and vicinity, and the Glacier National Park area (Finklin 1983a, 1983b, 1986).

The purpose of these reports is to provide climatic data for use in studies of fire history, fire effects, and prescribed burning in the areas described, and to support the application of fire management science and technology. More specifically, climatic data are helpful in establishing seasonal limits for prescribed burning. The data also form a baseline of "normals" from which deviations in particular years may be related to postfire vegetal response and other effects. The uses of this climatic data are not limited, however, to fire-related activities. Climate is an important variable in many forestry research studies and an important consideration in planning a variety of forestry activities, such as tree regeneration, insect and disease control, watershed protection and management, and recreation.

Our climatic analysis for Deception Creek Experimental Forest includes data from adjacent stations. The scope of this report therefore covers much of the Coeur d'Alene National Forest.

THE DECEPTION CREEK EXPERIMENTAL FOREST

The Deception Creek Experimental Forest was established in 1933 for research and demonstration purposes in the western white pine (*Pinus monticola*) forest cover type of the northern Idaho panhandle. Early research emphasis was on harvesting methods, stand improvement practices, artificial and natural regeneration techniques, and white pine blister rust control (Wellner and Foiles 1951). During subsequent years, studies relating to pole blight, growth and yield, forest hydrology, and root diseases have also been conducted by Intermountain Research Station scientists and university cooperators. Recent research has included investigation of fuel reduction and duff consumption by prescribed fires in spring, summer, and fall.

The Experimental Forest occupies 3,517 acres of the Fernan Ranger District, Coeur d'Alene National Forest. It is located about 14 air miles (22 road miles) east-northeast of Coeur d'Alene, ID, at about 47°45' N. latitude, 116°30'

W. longitude (fig. 1). Elevations within the Experimental Forest range from about 2,800 ft at the eastern edge along Deception Creek to 4,600 ft on ridges that form the northern and southern boundaries. Many small creeks drain north or south into Deception Creek, a tributary of the North Fork Coeur d'Alene River just east of the Experimental Forest boundary. The major tree species are western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), western white pine, western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*). Prevalent habitat types are of the western hemlock and the grand fir series (Cooper and others in press).



Figure 1—Location of Deception Creek Experimental Forest in northern Idaho, together with adjacent climatic stations and other places included or mentioned in this report.

STATIONS, DATA, AND METHODS

Although this climatic description utilizes the available Deception Creek data, it also depends upon stations in the surrounding area. The locations of these stations are shown in figure 2. Details concerning the stations, types and sources of data, and methods of analysis follow.

Deception Creek Headquarters Station

The primary Deception Creek station, referred to as headquarters, or Deception Creek, is at the experimental forest headquarters compound (fig. 3A). The site is in a sheltered clearing in the ravine bottom of Sands Creek, a tributary of Deception Creek, at an elevation of 3,060 ft. Headquarters data availability is outlined in table 1.

Additional data were collected in summer during the 1960's and some earlier and later years. The records could not be located, however, or were not in usable form (for example, hygrothermograph charts were lacking calibration checks). Fire-weather observations in this locale were initially taken, during 1933-35, at the former Honeysuckle Ranger Station. This station was located 1.3 miles north-east of present headquarters and about 300 ft lower in elevation; it was likewise in a sheltered setting. We cite for comparison some findings from the Honeysuckle data.

Other Stations

Remote Automatic Weather Station—A remote automatic weather station (RAWS) was operated during the summer and early fall of 1984 and 1985 in conjunction with fire research studies in the Blue Rock Creek drainage. The RAWS site (fig. 3B) is in a shrub-covered clear-cut on a north-facing slope at about 3,950 ft in elevation, 2 miles west-northwest of the headquarters station. Data are on file at the Intermountain Fire Sciences Laboratory and include hourly temperature, relative humidity, wind direction and speed, and precipitation.

Wolf Lodge Summit—During the 1940's a recording precipitation gage was in service on a heavily wooded ridge designated as Wolf Lodge Summit (U.S. Weather Bureau 1958b), 2 miles southwest of headquarters at an elevation of 4,650 ft (fig. 2). Precipitation amounts collected at this site during 1948 and 1949 fire seasons were published in monthly "Climatological Data" State summaries for Idaho. Earlier, year-round data were obtained from files at the Forestry Sciences Laboratory, Moscow, ID.

Lower Sands Creek and Copper Ridge Snow Courses—The Lower Sands Creek snow survey course, located near headquarters, has provided monthly snow depth and water content data from 1936 to the present.

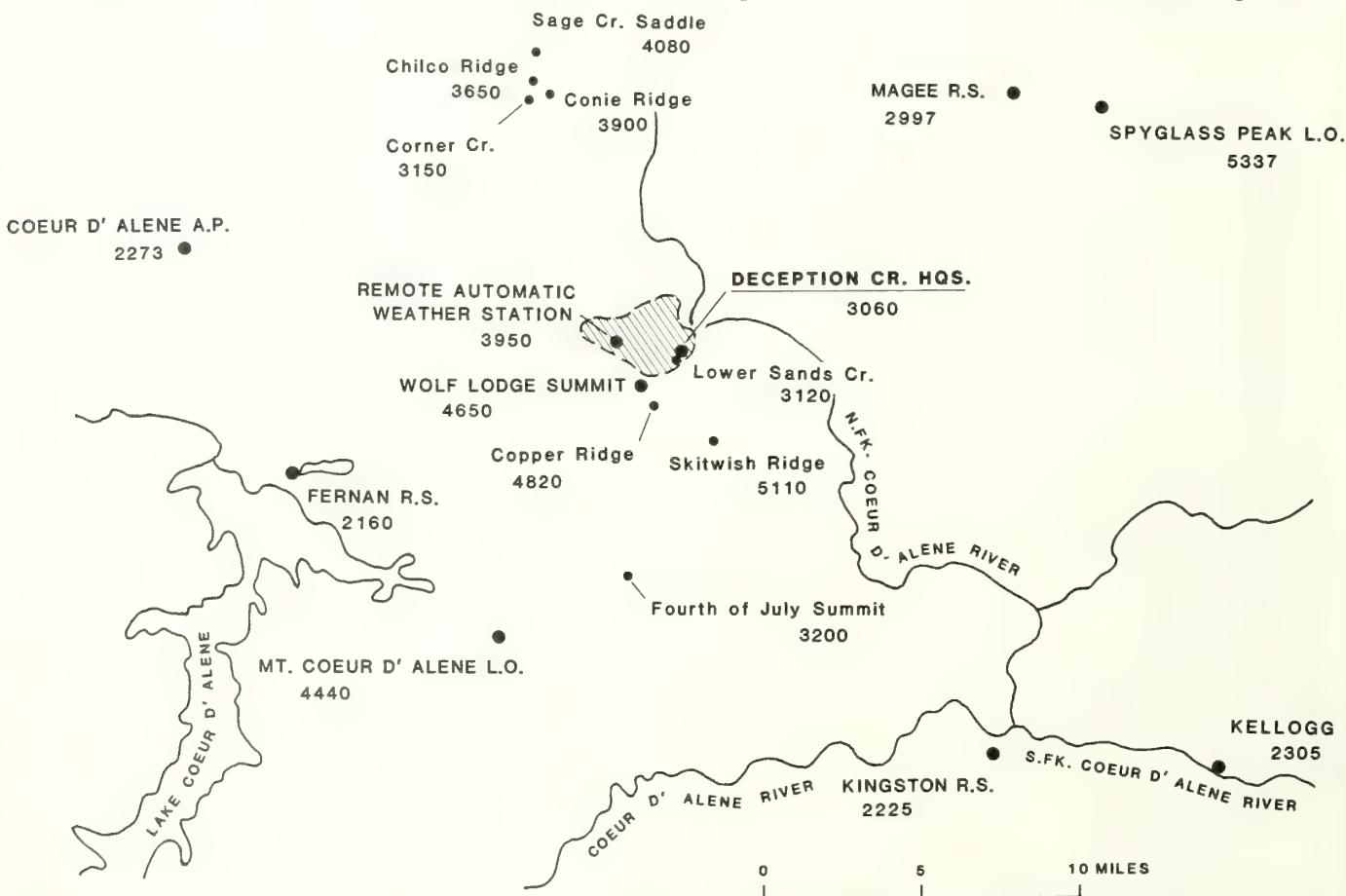


Figure 2—Location of stations used in this report, in or near Deception Creek Experimental Forest (shown by dashed outline and hatching). Includes climatic and fire-weather stations (upper case letters) and snow-survey courses (upper and lower case letters). Numbers are elevations in feet.



(A)



(B)



(C)

Figure 3—Weather observation sites in Deception Creek Experimental Forest, ID, shown in 1984. (A) Headquarters; equipment other than recording precipitation gage on post and relic wind vane was temporary, in use for fire research during summer and autumn 1984-85. (B) RAWS (Remote Automatic Weather Station), in use during 1984-85. (C) Sacramento-type storage precipitation gage, in headquarters clearing; gage has provided yearly precipitation totals since 1955.

Table 1—History of weather and climatic observations at Deception Creek headquarters for data used in this report

Type of station	Observation interval	Period of record	Data collected	Data source
Climatic station	Daily, year-round	1936-45	Maximum and minimum temperatures, precipitation, and snowfall.	U.S. Weather Bureau Climatological Data for Idaho; Wellner and Foiles (1951); U.S. Weather Bureau (1958a).
Fire weather station	Daily at 1630 P.s.t., May-October	1936-46	Wet and dry bulb temperature, wind speed and direction, cloud cover, state of weather, precipitation amount and duration, thunderstorm occurrence, maximum and minimum temperatures and relative humidities.	U.S. Weather Bureau forms 1009-E on file at the Intermountain Fire Sciences Lab, Missoula, MT.
Recording rain gage	Hourly, May-October	1944-present	Precipitation amount and duration.	U.S. Weather Bureau (and successor agencies) Climatological Data (1948-51); Hourly precipitation data (1951-70).
Storage gage	Annual	1955-present	Precipitation amount.	U.S. Weather Bureau (and successor agencies) Storage-Gage Precipitation Data for the Western United States (1955-76).
Fire research station	Hourly, June-October	1984-85	Temperature, relative humidity, and precipitation and amount and duration.	Hygrothermograph and recording rain gage charts on file at the Intermountain Fire Sciences Lab, Missoula.

Measurements, mostly taken about March 1, April 1, and May 1 of each year, were obtained from the U.S. Department of Agriculture, Soil Conservation Service (ca. 1980) and its monthly "Water Supply Outlook" for Idaho. Similar measurements were obtained for a ridge site, Copper Ridge snow course, at 4,820 ft, near the former Wolf Lodge Summit station.

Adjacent Stations—Data sources for the adjacent stations (figs. 1 and 2) are those already mentioned and also later climatic publications. Sources include the National Oceanic and Atmospheric Administration (1982), the National Fire-Weather Data Library (Furman and Brink 1975), and the Pacific Northwest River Basins Commission (1968).

The nearest long-term climatic stations, situated in valley bottoms, are at Coeur d'Alene and Kellogg, ID. Continuous records date from 1914 and 1905, respectively, though several changes have occurred in station location, adversely affecting data homogeneity (Landsberg 1958; Finklin 1983a). The Coeur d'Alene station was at nearby Gibbs during 1925-39 (close to the western city limits),

before its move in 1939 to Fernan Ranger Station (near the southeast edge of Coeur d'Alene). The climatic station was terminated here in 1986 and moved to the somewhat distant Coeur d'Alene airport.

The Kellogg station was at its original site in town for 60 years, until late 1965, when it was relocated 3 miles west to the Kellogg (Shoshone County) airport. It was moved back to the edge of town in 1970, and smaller moves occurred in 1975 and 1986. The Kellogg airport records indicated some much lower minimum temperatures and less precipitation than would have been recorded in town.

Fire weather data have been recorded at Fernan Ranger Station, during May-October, since 1939. Kingston Ranger Station provided such data from 1937 through 1972; Magee Ranger Station only from 1963 through 1972 and for a shorter season. Data from the Mount Coeur d'Alene and Spyglass Peak Lookouts were also discontinued in the early 1970's, after about 20 to 25 years of record. These records are limited mostly to July and August.

Data Analysis

The climatic and fire-weather data were summarized by use of computer programs described by Bradshaw and Fischer (1984). The resulting summary tables for Deception Creek headquarters and for several adjacent valley and mountaintop stations are given in the appendix. These tables may cover differing periods of record, governed by data availability and changes in observation time. Before the year 1950, fire-weather observations were taken near 1630 (4:30 p.m.), P.s.t. Thence through 1973, the observation time was near 1500 (3:00 p.m.). In 1974, the time changed to 1200 (noon), to conform with a national standard. This 3-hour change has affected the comparability of recent data with past data, as shown in a later section.

For the climatic values used in our figures and text, the averages from short and differing periods of record were adjusted to standard or longer term normal periods. This adjustment, described by Finklin (1983a), employs the "difference method" for temperature and relative humidity and the "ratio method" for precipitation. Generally, data from between three and five adjacent stations were involved in each adjustment calculation. This practice should help reduce or smooth out adjustment errors resulting from nonhomogeneous data at the individual stations. As adopted by international convention, the standard normals are based on a 30-year period, currently 1951-80, but we have used a 50-year period, 1931-80, which includes the actual years of observations at Deception Creek. The longer period is desirable at least for precipitation (World Meteorological Organization 1967), affording a more stable and representative baseline, as precipitation values can vary considerably between years and decades.

SUMMARY OF CLIMATE

The general climate of the Idaho panhandle is transitional between a north Pacific coastal type and a continental type. The Pacific influence is particularly noted by an autumn and winter maximum in low-type cloudiness and precipitation. These are enhanced by the mountainous topography and its forced uplift of moist airflow.

The lifting or orographic effect is strongly evident at Deception Creek, where average annual precipitation, adjusted to a 1931-80 normal period, is about 55 inches at headquarters. In comparison, the adjacent valley-located climatic stations in northern Idaho average 26 to 42 inches. About 10 percent additional annual precipitation is indicated on Wolf Lodge Ridge, near the southern edge of Deception Creek Experimental Forest.

The cloudiest, wettest months are usually November, December, and January. These three months have precipitation averages between 7 and 9 inches. Sunshine in December averages only about 20 percent of the maximum possible.

Annual snowfall at Deception Creek headquarters averages 160 inches, which in water content represents about 25 percent of the total precipitation. Snow cover near headquarters is usually continuous from sometime in November to late April or early May. Seasonal maximum depth here is usually reached in February or March and

averages 5 to 6 ft. Seasonal maximum depth averages about 7 ft on Wolf Lodge Ridge.

Monthly average precipitation gradually decreases during spring at Deception Creek but is still about 3.00 inch in June. A pronounced clearing and drying follows in July with 50-year average precipitation close to 1.00 inch. July sunshine averages near 80 percent of the maximum possible, compared with about 60 percent in June. Sunny, dry conditions normally continue during much of August, but precipitation averages about 0.75 inch during the final 10 days of the month. Autumn is usually well established by October, with monthly precipitation averaging nearly 5.00 inches.

Thunderstorms occur on an average of about 3 days per month in June, July, and August. Fifty percent of the June and August storms observed from Mount Coeur d'Alene Lookout began during the 6-hour period between 1600 and 2159 P.s.t.

Monthly average temperatures at headquarters range from 23 °F in January to 62 °F in July, based on a 24-hour period ending about 1630 P.s.t. and adjusted to 1931-80. The annual average is 42 °F, which is 5 to 6 °F below the average at adjacent Coeur d'Alene and Kellogg, ID, and 2 °F below the average at Priest River Experimental Forest headquarters. Average daily maximum readings at Deception Creek range from 29 °F in January to 81 °F in July. The corresponding minimums range from 16 °F to 43 °F. Extreme daily values, over a 50-year period, may range from -40 to 103 °F.

Frost (32 °F minimum temperature) occurs in the sheltered headquarters ravine bottom in July and August in many years. This location has an average period of about 125 days between killing frosts (28 °F minimum temperature or lower), extending from late May to late September.

On adjacent slopes and ridges, fair-weather nighttime temperatures are typically higher than those at the bottom, and the frost-free periods may average 1 to 2 months longer. Minimum temperatures at the Remote Automatic Weather Station (RAWS) during July-August 1984 averaged 5 °F higher than the minimums at headquarters, with an extreme difference of 12 °F.

Afternoon relative humidity at Deception Creek averages near or above 80 percent during November, December, and January. This decreases to about 50 to 55 percent in May and June and to below 40 percent in July and August. By early August, however, relative humidity in the headquarters area typically undergoes a large diurnal increase by 1700 P.s.t., together with a temperature decrease. This local characteristic is an effect of shading by nearby terrain and trees—and resulting radiational cooling.

On an open slope at 4,000 ft, midafternoon relative humidity below 30 percent normally occurs on about 5 to 6 percent of the days during May-early June, increasing to 50 percent of the days in late July. This frequency decreases to 10 percent in late September.

Large-scale windflow over the Idaho panhandle is typically from the west or southwest throughout the year but direction and speed are modified by the terrain. During July and August, ranger stations and lookouts in the Coeur d'Alene National Forest area have midafternoon

windspeeds averaging mostly 5 to 6 mi/h. Observed speeds averaged only half as great at Deception Creek headquarters. The standard 10-minute average speeds were not often high even at the lookout stations, but 1985 data from the RAWS site illustrate the higher speeds that may possibly occur during gusts. Peak gusts at this site on July-August early afternoons averaged 15 mi/h, compared with hourly reported 10-minute speeds averaging 5 mi/h.

Downslope and downcanyon airflows, or drainage breezes, often occur during fair-weather nighttime hours. These local winds are usually very light, as was observed at the RAWS north-slope site.

DETAILS OF THE CLIMATE

Cloudiness and Sunshine

The period November through February is normally the cloudiest time of year in the Idaho panhandle; July and August, the clearest. The adjacent Spokane and Kalispell National Weather Service Stations have an average of only 3 or 4 clear days per month during the above autumn-winter period. This number slowly increases to 8 days in June and then jumps to 17 days in July and 16 days in August. Clear days are defined as those days with sunrise-to-sunset cloud cover of any type averaging 0 to 3 tenths. The corresponding frequency of cloudy days—those with cloud cover averaging 8 to 10 tenths—peaks at about 24 days in December. This decreases to 12 days in June and to 6 or 7 days in July and August.

The 1936-45 observations at Deception Creek show about two additional clear days and two fewer cloudy days per month in autumn and winter than are found in the Spokane or Kalispell averages. This difference may arise from classifying as clear or partly cloudy some of those days with high, thin (cirrus-type) clouds, through which the sun can shine.

Average sunshine occurrence in this area ranges from about 20 percent of maximum possible in December to near 80 percent in July. On open flat terrain (if it existed), the corresponding monthly total hours of sunshine would range from about 50 to 375. The annual regime, portrayed in figure 4, reflects the large decrease in cloudiness between June and July.

Precipitation

Annual Regime—The long-term average annual precipitation at Deception Creek, based on the 50 years 1931-80, is about 56 inches (rain and melted snow). This estimate is several inches greater than the average during the relatively dry 1936-45 period of observation (table 2). Observed annual totals ranged from 37 inches in calendar year 1944 to 69 inches in 1945. The storage gage measurements (fig. 3C) gave a 20-year, 1955-74 average of 54 inches.

As indicated in table 2 and in figure 5, Deception Creek is much wetter than the neighboring valley stations at Coeur d'Alene and Kellogg, which have annual averages between 26 and 31 inches. About 42 inches occurs in the valley farther east at Wallace, ID. Deception Creek's heavy precipitation apparently includes much spillover

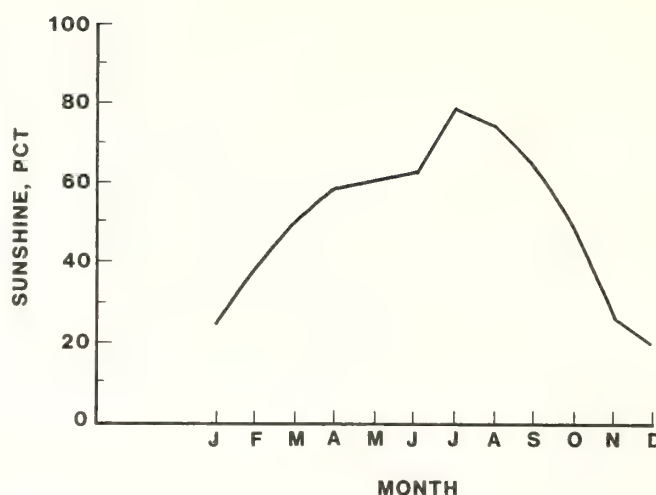


Figure 4—Monthly average percentage of maximum possible sunshine duration estimated for Deception Creek area. Interpolated from long records at Spokane, WA, and Kalispell, MT, and maps by Environmental Sciences Services Administration (1968).

from the nearby mountainous terrain, where precipitation increases may be expected from the forced lift of moist airflow (Schroeder and Buck 1970). (Spillover is an effect of winds aloft on precipitation trajectories.) Recordings from Wolf Lodge Summit for 2 complete years (December 1941 through February 1944) indicate 10 percent greater annual precipitation there than at the headquarters station.

The Deception Creek averages are approached and exceeded in the more general area of heavy precipitation near the Idaho-Montana border (the Bitterroot Divide). The former (1921-53) climatic station at Roland, ID, elevation 4,150 ft, 14 miles east-southeast of Wallace, has an estimated 1931-80 annual average of 54 to 55 inches.

The long-term average monthly totals at Deception Creek headquarters reach between roughly 7 and 9 inches during November through January, with the peak occurring in December. Averages during spring taper off from 4 inches in April to 3 inches in June, followed by a sharp decrease to 1 inch in July. An increase normally starts in August, leading to an average of 5 inches in October.

A listing of the monthly and annual precipitation for each year of Deception Creek's 1936-45 record is given in table 5 (appendix). Listings, covering a much longer period through 1985, are also given for Coeur d'Alene and Kellogg. Although these two stations are drier and data may be affected by site changes, they should give a general indication of the relatively wet and dry months and years in the Deception Creek area. There appears to be a good areal correlation of annual amounts. For the 9 complete years, 1937-45, the linear correlation coefficient r , obtained between the Deception Creek and Coeur d'Alene amounts, was 0.87; between Deception Creek and Kellogg, it was 0.92.

The 10-year monthly extreme totals at Deception Creek (table 5, appendix) ranged from zero in July 1945 to 14.02 inches in November 1937. The storage gage measurements during 1955-74, taken at approximately monthly intervals

Table 2—Monthly and annual average precipitation (Ppcn) and snowfall (Snow) at Deception Creek headquarters, as observed during period June 1936 to October 1945 and adjusted (see text) to 50 years, 1931-80. Comparative 1931-80 averages given for adjacent stations in Idaho panhandle; observed 50-year values except for indicated adjustments or estimates from shorter records. Estimates made for missing daily and monthly data. T denotes trace

Station and elevation (ft)		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
----- Inches -----														
Deception Creek, 3,060														
Observed	Ppcn	5.14	5.80	5.34	4.52	3.64	3.25	0.77	1.01	2.92	4.76	6.18	8.36	51.69
1936-45	Snow	30.1	34.3	14.2	2.6	0.3	T	0	0	0	1.3	16.8	28.0	127.6
Adj. to 50 yrs	Ppcn	7.80	5.90	5.65	4.05	3.50	2.95	1.00	1.48	2.50	4.80	7.30	8.90	55.83
1931-80	Snow	47.5	27.5	17.0	2.5	0.3	T	0	0	T	2.0	22.2	40.8	159.8
Burke (2 ENE) ¹ 4,093														
	Ppcn	6.98	5.50	5.20	3.33	2.95	3.35	1.05	1.30	2.55	3.97	5.47	7.15	48.80
	Snow	65.0	46.0	39.0	12.5	5.0	0.1	0	0	0.1	4.0	27.0	53.0	251.7
Coeur d'Alene 2,160														
	Ppcn	3.58	2.50	2.28	1.68	2.02	1.93	0.70	0.99	1.25	2.10	3.10	3.81	25.94
	Snow	19.3	10.5	3.9	0.3	T	0	0	0	0	0.2	4.7	13.5	52.4
Kellogg 2,305														
	Ppcn ²	3.95	2.95	2.83	2.33	2.37	2.31	0.89	1.07	1.70	2.64	3.46	4.13	30.63
	Snow	20.0	10.8	6.3	0.6	T	0	0	0	0	0.3	5.0	14.8	57.8
Kingston Ranger Sta. 2,225														
	Ppcn ³					2.21	2.15	0.78	1.11	1.77	2.40			⁴ 29.75
Magee Ranger Sta. 2,997														
	Ppcn ⁵						2.35	0.90	1.22	2.00				
Priest River Exp. For. 2,380														
	Ppcn	4.28	3.10	2.75	2.01	2.28	2.31	0.99	1.15	1.59	2.82	4.03	4.86	32.17
	Snow	29.1	15.8	6.9	0.6	0.1	0	0	0	T	0.8	10.2	24.9	88.4
St. Maries 2,145														
	Ppcn	4.09	2.93	2.68	2.08	2.02	2.08	0.77	0.99	1.35	2.37	3.51	4.27	29.14
	Snow	18.0	7.8	4.2	0.4	T	0	0	0	T	0.4	4.6	12.9	48.3
Sandpoint 2,100														
	Ppcn	4.39	3.30	2.81	2.00	2.20	2.21	0.84	1.20	1.70	2.97	4.27	5.00	32.89
	Snow	25.6	15.8	7.2	0.8	T	0	0	0	T	0.7	7.1	21.4	78.6
Wallace 2,770														
	Ppcn ⁶	5.95	4.50	3.85	2.73	2.57	2.70	1.10	1.22	2.17	3.60	5.23	6.43	42.05
Wallace (2 NE), Woodland Park 2,950														
	Ppcn	5.01	3.68	3.51	2.53	2.48	2.65	1.06	1.19	1.98	3.20	4.39	5.33	37.00
	Snow ⁷	27.8	19.3	14.0	2.4	0.4	T	0	0	T	0.5	8.3	22.3	95.0

¹Located 9 miles northeast of Wallace. Averages estimated from 1946-67 data.

²Adjusted for 4 or 5 years, 1966-70, when station was at airport (see text).

³Estimated from 1941-70 data.

⁴Estimated using Coeur d'Alene-Kellogg average ratio of May-October/annual precipitation.

⁵Estimated from 1963-72 data.

⁶Estimated from 1921-60 data.

⁷Slight adjustment made for incompatibly high 1931-40 snowfall averages.

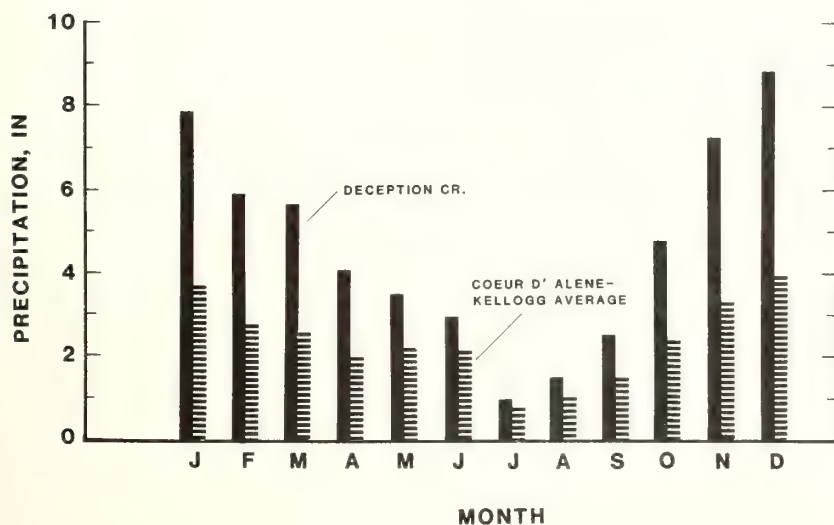


Figure 5—Average monthly precipitation, inches, at Deception Creek headquarters; adjusted to 50-year period 1931-80. Comparative average at adjacent Coeur d'Alene and Kellogg, ID (two-station average).

in a few of the years, show 19.20 inches precipitation in the 39 days from December 12, 1973, to January 20, 1974; 30.70 inches between November 13, 1973, and January 20, 1974. Coeur d'Alene received 8.94 inches and 14.62 inches during the respective periods.

Snowfall—The 50-year average annual snowfall at Deception Creek headquarters (table 2) is about 160 inches; like total precipitation, this is higher than the observed 1936-45 average. Seasonal snowfall during the 10 years of record ranged from 63 inches in 1939-40 to 208 inches in 1938-39. The 50-year monthly averages reach between 40 and 50 inches in December and January. Peak average snowfall occurs in January, when a larger portion of the total precipitation occurs as snow. Much of the winter precipitation still occurs as rain. Overall, snowfall contributes little more than 25 percent of the annual total precipitation at headquarters. The contribution should reach 50 percent at 5,000-ft elevations in the Experimental Forest vicinity (Finklin 1983b), with probably over 300 inches of snowfall. Near the Idaho-Montana border, the former station locations at Burke (2 ENE) and Roland, at only 4,100 to 4,150 ft, have average annual snowfall of close to 250 inches and 300 inches, respectively.

Snowpack—Snow cover at headquarters is usually continuous from sometime in November to late April. The snow attains an average seasonal maximum depth of between 5 and 6 ft, usually in February or March. A 1937-45 comparison indicates similar depths at headquarters and the nearby Lower Sands Creek snow-survey course until around March 1, but afterwards headquarters has lower depths and earlier melt. Snow usually lingers on the snow course through early May.

Snow survey data are summarized in table 3; data are included for Copper Ridge, on the Wolf Lodge Divide. Snowpack at the ridge location may reach an average seasonal maximum depth of 7 ft, which is somewhat greater than the maximum based on the fixed monthly snow survey dates. Here, the monthly values average greatest on the April 1 survey date, with snow depth 72 inches and water content 29 inches. A comparison in figure 6, with April 1 data at adjacent snow courses, further indicates that Deception Creek (Lower Sands Creek) is wet and snowy for its elevation. Its snow depth averages 56 inches, water content 21 inches. The greater

precipitation on nearby ridges is shown particularly at Skitwish Ridge, where the April 1 average snowpack water content is 36 inches.

Extreme Daily Precipitation—During 1936-45, 24-hour precipitation at Deception Creek exceeded 2.00 inches on 11 occasions. Highest observed daily total was 4.17 inches on October 31, 1942. On that day, however, the total at Wolf Lodge Summit was just 1.87 inches. Wolf Lodge recorded 3.05 inches on April 1, 1942, on which day Deception Creek had 2.69 inches. In contrast, at Coeur d'Alene during the 50 years 1931-80, daily precipitation exceeded 2.00 inches only twice (tables 6 and 7, appendix). The extreme was 2.19 inches in January 1954.

Maximum 24-hour snowfall at headquarters during 1936-45 was 15 inches. A 2-day total reached 27 inches, observed in December 1937. Greatest 2-day total at Coeur d'Alene during 1931-80 was 19 inches in February 1955; at Priest River, 25 inches in January 1950.

Precipitation During Fire Season—The May through October precipitation at Deception Creek is plotted by 10 (or 11)-day periods in figure 7. The period averages are estimated from the already derived 1931-80 monthly averages; 10-day apportionment was interpolated from adjacent climatic stations for which 50-year, 10-day averages had been previously calculated.

The 10-day average precipitation appears to reach a late-spring maximum of about 1.20 inches during late May and early June. A minimum of 0.25 inches occurs during late July and early August. The irregularities seen in the autumn precipitation increase are found in the 50 years of actual data at the adjacent stations. This peculiarity may be an accidental effect related to precipitation's great variability.

The portrayed frequencies of daily and 10-day amounts (fig. 7) closely follow the trend of the averages—perhaps too closely, as they are estimates derived from a relationship with the averages. A frequency-versus-average diagram (Finklin 1983a) was drawn from the 1936-45 fire-season data (treated with 3-point smoothing) and then entered at the 1931-80 average values. The estimates, representing long-term probabilities, indicate that the chance of a 10-day accumulation ≥ 0.50 inch decreases from about 75 percent in late May and early June to 22 percent in late July and early August. It again reaches 75

Table 3—Snow survey data in Deception Creek area. Average snow depth and water content, inches, and snowpack density measured near first day of month; based on period 1951-85. Maximum and minimum amounts are those observed since 1937

Snow course and elevation	Survey date	Snow depth					Water content					Snowpack density ¹
		Average	Maximum		Minimum		Average	Maximum		Minimum		
		Inches	Inches	Year	Inches	Year	Inches	Inches	Year	Inches	Year	
Lower Sands Creek 3,120 ft	March 1	55	100	1956	12	1981	17.9	28.6	1974	4.1	1981	0.33
	April 1	56	89	1974	8	1940	21.0	33.9	1974	3.6	1940	.38
	May 1	37	73	1974	0	1981 + ²	15.9	31.1	1964	0	1981 +	.43
Copper Ridge 4,820 ft	March 1	69	127	1974	21	1981	24.6	47.2	1974	7.6	1981	.35
	April 1	72	107	1949	17	1981	28.6	45.9	1949	3.6	1981	.40
	May 1	53	94	1950	0	1981 +	24.6	43.4	1972	0	1981 +	.46

¹Snowpack density is equal to water content divided by snow depth.

²+ Denotes occurrence of same value in earlier years.

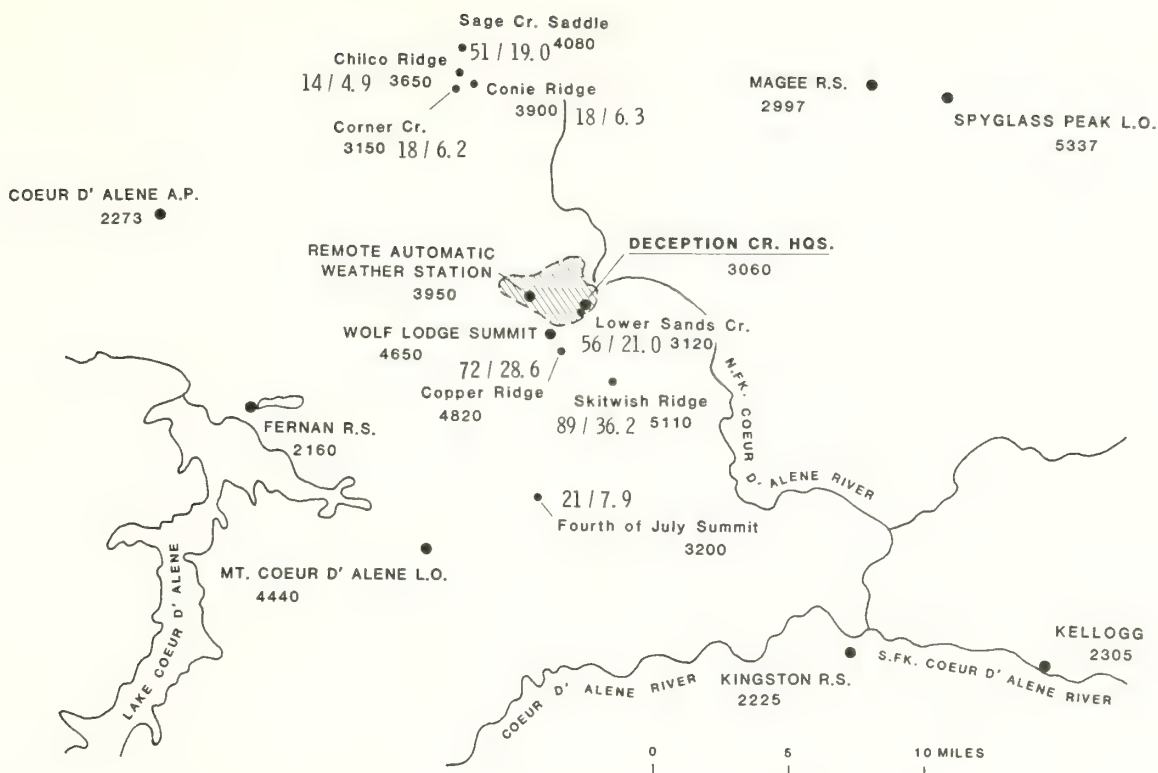


Figure 6—Average snow depth (number to left of slash) and water content, inches, on about April 1 at snow-survey courses in Deception Creek vicinity; based on or adjusted to 35 years 1951-85.

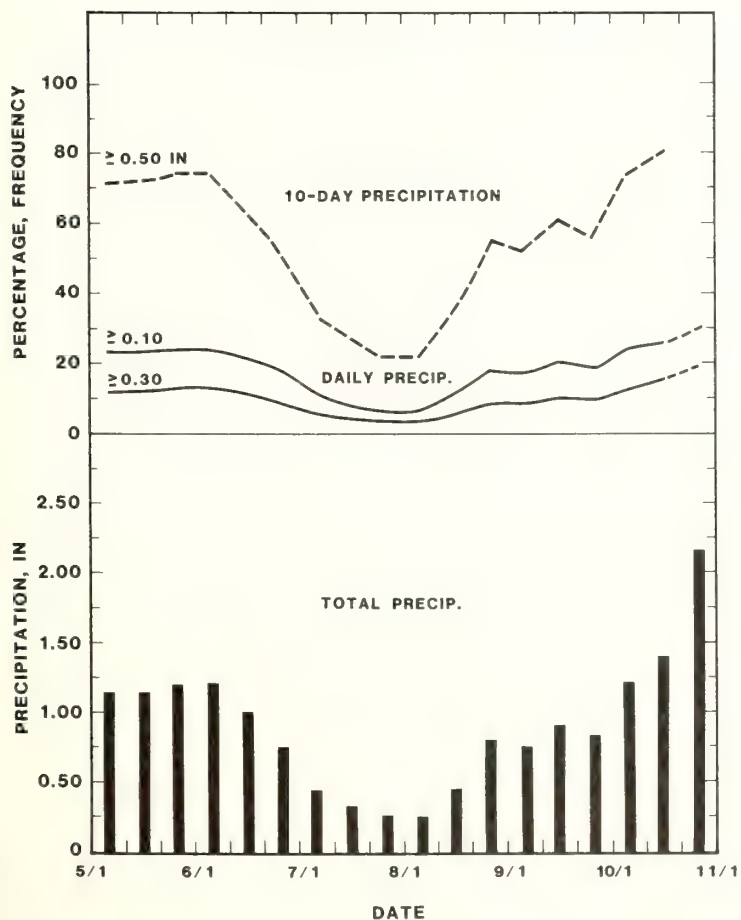


Figure 7—Precipitation, inches, by 10 (or 11)-day periods during May to October at Deception Creek headquarters; adjusted and estimated for 50-year period 1931-80 from mostly 1936-45 data (see text). Lower panel: Average totals. Upper panel: Percentage frequency of specified daily and 10-day amounts.

percent in early October. Chance of daily rainfall ≥ 0.10 inch correspondingly varies between 25 percent and 6 percent.

Statistical details of the observed fire-season precipitation are given in table 6 (appendix). As previously indicated, the 10-year Deception Creek data should not be quoted for long-term representation. Details covering the entire year are included for Coeur d'Alene. These are based on 50 years but represent a much drier location. Frequencies of various daily amounts are shown in table 7 (appendix).

July and August precipitation averages in the Coeur d'Alene National Forest area are mapped in figure 8. As was indicated in figure 5, the summertime amounts at Deception Creek headquarters are only slightly above those at the adjacent stations. The averages show a slight elevational increase between the ranger stations and their nearby lookouts. This was also found in other parts of Idaho (Finklin 1983b, 1983c). Such an increase is probably also characteristic in the Deception Creek area, based on the available data from Wolf Lodge Summit. July-August precipitation for 4 years (1942, 1943, 1948, and 1949) was 9 percent greater at Wolf Lodge, averaging 3.39 inches versus 3.11 inches at headquarters.

No such elevational increase was recorded at the Deception Creek RAWS site, where precipitation data were available only during July to mid-October 1984. During this period, the RAWS accumulation totaled only one-half of that at headquarters (2.27 inches versus 4.39 inches). For such a discrepancy, we can suspect random factors in the short period of record and possible gage deficiency. Greater wind at the more exposed RAWS site may have

reduced some of the gage catch (Linsley and others 1958; Brown and Peck 1962). Most of the precipitation occurred in September and October, but there appears to have been little snow involved at RAWS. The RAWS gage, of a tipping-bucket type, is not suitable for collection of snow. The recording gage at Wolf Lodge Summit, of a universal weighing type, was in a wooded location and apparently sheltered from the wind.

Thunderstorms—June, July, and August are normally the peak months of lightning (thunderstorm) activity in the Idaho panhandle. This section will cover only July and August, the months of greatest storm data availability from lookouts and greatest occurrence of lightning-caused fires.

Observations from Mount Coeur d'Alene and Spyglass Peak indicate an average of 6 or 7 thunderstorm days during July and August combined. This average refers to storms within about a 20-mile radius. In individual years, during about 20 years of record, the number of July-August thunderstorm days ranged from a minimum of one or two to a maximum of 12 (at Spyglass in 1961).

The more detailed Mount Coeur d'Alene observations show that 25 percent of 92 tabulated storms began between midnight and noon (0000-1159 P.s.t.), 75 percent between noon and midnight (1200-2359). We have arbitrarily defined individual storm cases by at least 3 hours time separation between reported lightning or thunder occurrence. One-half of these storms (51 percent) began during the 6-hour period 1600-2159 P.s.t., with 26 percent during a peak 2-hour period from 1900 to 2059 P.s.t.

The Lightning Activity Level (Deeming and others 1977) may reach "5" in 12 percent of the July-August storms.

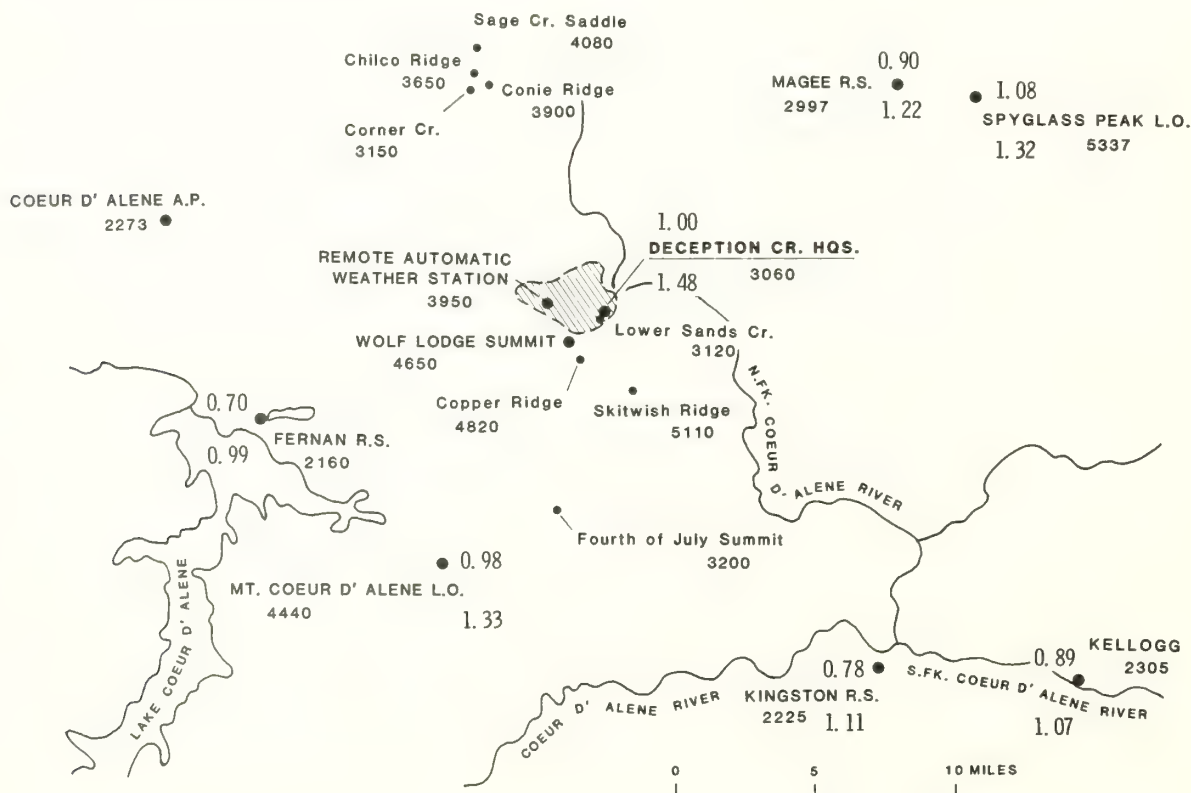


Figure 8—Average precipitation, inches, during July (top number) and August (bottom number), based on or adjusted to 50-year period 1931-80.

This is based on maximum 15-minute counts of cloud-to-ground lightning observed from Mount Coeur d'Alene during 1960-70, in 50 available cases (data on file at the Intermountain Fire Sciences Laboratory). The level was a milder "2" in 62 percent of these storms and "3" in 20 percent.

Precipitation Trends—Precipitation trends or fluctuations during the past 70 years, in the area adjacent to Deception Creek, are indicated in figure 9 using successive 5-year averages. Derivation is described in the figure legend. The graph of annual precipitation shows the extended dry period that covered the 1920's through the early 1940's. The 5-year averages for 1921-25 and 1926-30 were 86 to 87 percent of the 50-year (1931-80) average. Alternating wet and dry periods have occurred following a recovery in the later 1940's, but little overall trend is suggested since 1950.

The annual precipitation behavior is reflected somewhat in the winter season graphs (for November-December and January-February), though these exhibit greater swings or

percentage deviations from the long-term average. The late spring (May-June) and summer (July-August) graphs also show dry conditions in the 1920's and 1930's, but autumn (September-October) precipitation was generally above average during the 1930's. Many opposing fluctuations are seen between the different seasons. May-June precipitation shows a 1941-45 peak amounting to 130 percent of average, while January-February and July-August amounts were less than 70 percent of average. More recently, the summer precipitation reached 172 percent of average during 1976-80, while September-October precipitation bottomed at 65 percent.

Temperature and Relative Humidity

Annual Regime, Temperature—The course of monthly average temperatures at Deception Creek headquarters is portrayed in figure 10. The adjusted, 50-year average maximums range from 29 °F in January to 81 °F in July. The corresponding minimums range from 16 to 43 °F.

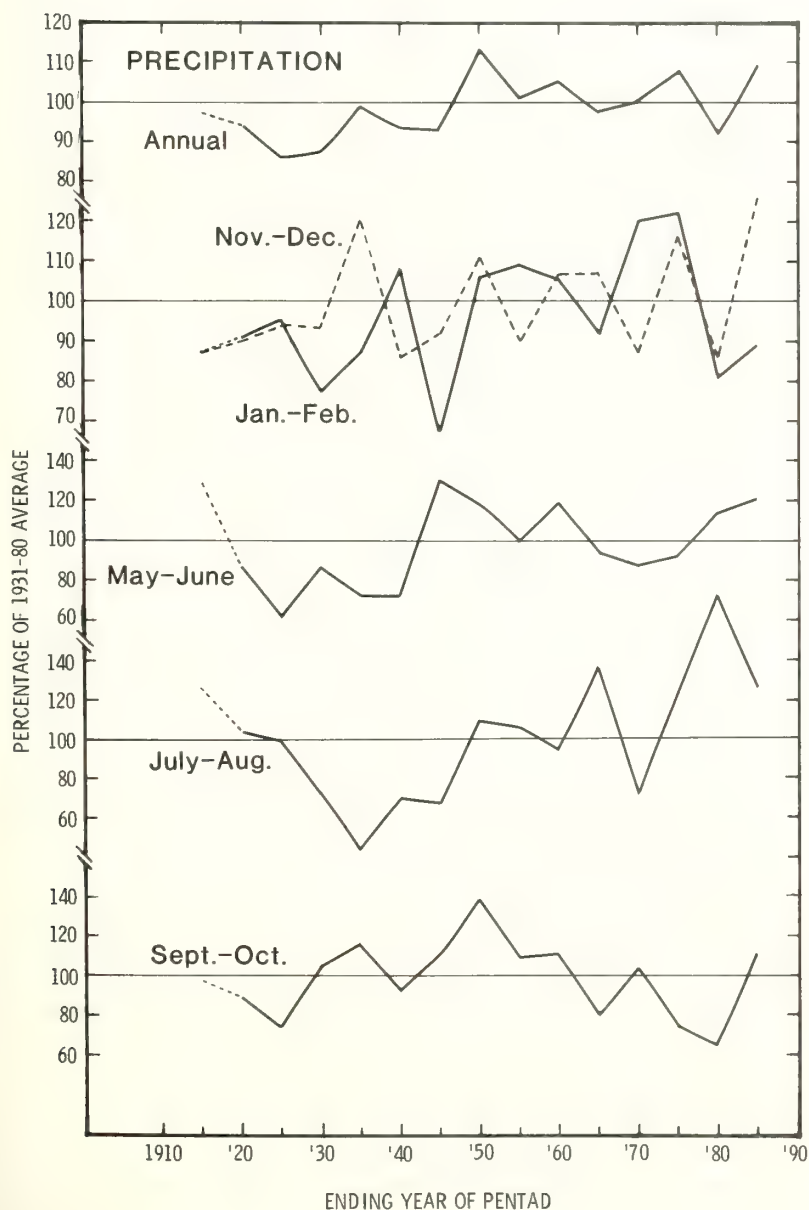


Figure 9—Fluctuations of annual and seasonal precipitation since 1910's in northern Idaho area adjacent to Deception Creek; shown by successive 5-year (pentad) averages for periods 1911-15 through 1981-85, plotted at ending years of periods. Values are given in percentages of 50-year, 1931-80, average precipitation. Based on weighted averaging of percentages obtained for each of five stations: Coeur d'Alene, Kellogg, St. Maries, Sandpoint, and Priest River. Designating these station percentages as letters A through E, respectively, formula employed for averaging was $\frac{1}{2} \{ \frac{1}{2}(A+B) + \frac{1}{4}(A+B+C) + \frac{1}{2}(D+E) \}$. Only B, D, and E were available for 1911-15 segment (short-dashed line). The averaging may smooth out data nonhomogeneities at the individual stations, but adjustment was made for the Kellogg data during 1966-70 (see text).

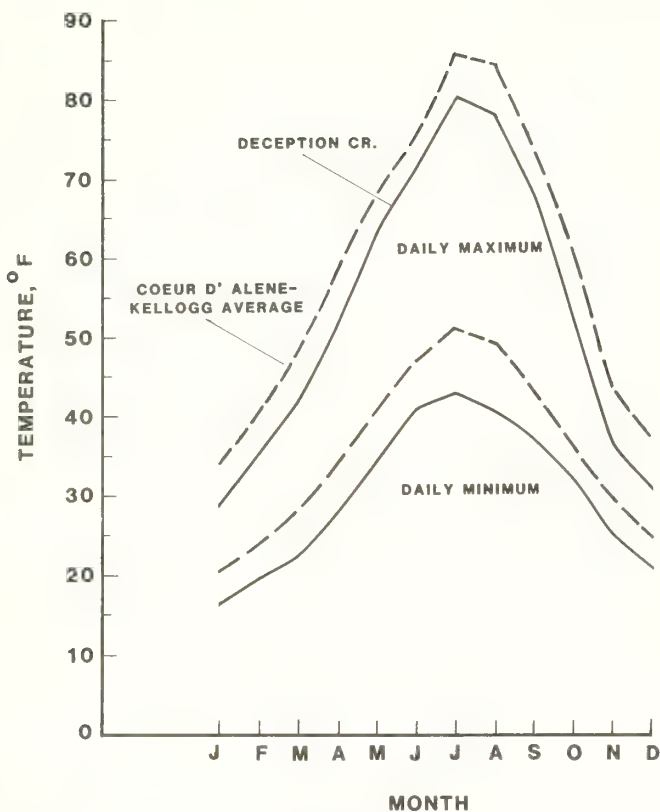


Figure 10—Average daily maximum and minimum temperatures, degrees Fahrenheit, annual regime, at Deception Creek headquarters (solid line), adjusted to 50-year period 1931-80; based on 1936-45 data, for 24 hours ending about 1630 P.s.t. Comparative averages observed at adjacent stations, Coeur d'Alene Ranger Station and Kellogg (two-station average) (dashed line).

Based on a 24-hour period ending at about 1630 P.s.t., the averages may run 1 or 2 °F higher than those based on the actual calendar day, particularly for spring and summer maximums (Finklin 1983a).

A comparison between Deception Creek and Coeur d'Alene-Kellogg graphs (fig. 10) shows generally parallel courses, though Deception Creek averages about 6 °F cooler overall. The elevation difference is only 800 to 900 ft. Temperature differences are greatest for July-August minimums, which average about 8 °F lower at Deception Creek. The cool summer nights here are associated with temperature inversions that are typical in fair weather. The sheltered ravine-bottom clearing favors ponding of cool-air drainage (Schroeder and Buck 1970; MacHattie and Schnelle 1974).

The annual mean temperature at Deception Creek is 42 °F. This represents an arithmetic average of the maximum and minimum values. Details of the monthly aver-

ages here and at adjacent stations are given in table 4. Monthly mean temperatures similar to those at Deception Creek are indicated during the fire season at the former Magee Ranger Station, with slightly higher maximums and slightly lower minimums. At the former Honeysuckle Ranger Station site, in July and August both maximum and minimum temperatures may average 1 or 2 °F higher than at nearby headquarters. This is indicated by respective 1933-35 and 1936-38 "difference-method" comparisons with five long-term stations.

The monthly and annual mean temperatures are listed in table 8 (appendix) for each year of record at Deception Creek (1936-45), Coeur d'Alene, and Kellogg. Statistical summaries pertaining to the maximum and minimum temperatures are given in table 9 (appendix). Corresponding frequency distributions of daily values are given in table 10 (appendix).

Daily Extremes—Extreme temperatures at Deception Creek headquarters over a 50-year period may range from about -40 to 103 °F. In the 1936-45 record, observed values ranged from -36 °F in February 1936 to 98 °F in July 1941. The Honeysuckle Ranger Station reached 103 °F in July 1934. On the same day Coeur d'Alene and Kellogg had 108 and 109 °F, respectively. Coeur d'Alene and Kellogg had 109 °F and 111 °F, respectively, in August 1961.

Frost-free Period—The Deception Creek headquarters area is subject to frost even in midsummer. During 1936-45, minimum temperatures of 32 °F or lower occurred in July (as late as July 31) in five of the years; in August (as early as August 3), in eight of the years. The 10-year average date of the last killing frost (28 °F minimum or lower) in spring was May 19. The date of the first killing frost in autumn was October 1. In individual years, however, these dates varied from April 29 to June 9 and August 28 to November 12, respectively. Honeysuckle Ranger Station had a 28 °F temperature as early as August 16 in 1935.

Adjusted to a longer, 50-year period of record (1931-80), the average killing frost dates at headquarters are about May 21 and September 23. This frost-free period thus averages 125 days, or about 1 month shorter on each end than the Coeur d'Alene and Kellogg average (April 20 and October 18). It is fairly similar to the 50-year average at Priest River Experimental Forest headquarters, May 11 to September 24. An apparently shorter frost-free season occurs at the Magee Ranger Station site, as reflected in the low average summertime minimum temperatures (table 4).

The frost-free periods for 28 °F and 32 °F thresholds may be 1 to 2 months longer under a full timber canopy in bottom locations, as indicated at Priest River (Finklin 1983c), and also on nearby slopes with their thermal-belt conditions (Schroeder and Buck 1970). No findings for Deception Creek slope areas can be drawn from the limited RAWs data.

Table 4—Monthly average temperatures, degrees Fahrenheit, at Deception Creek headquarters, as observed during period January 1936 to November 1945 and adjusted (Adj.) to 50 years 1931-80; based on 24-hour period ending about 1630 P.s.t. Mean is arithmetic average of maximum and minimum values. Comparative 1931-80 averages given for adjacent stations in Idaho panhandle; observed 50-year values except for indicated adjustments or estimates. Station elevations shown in table 2

Station		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Deception Creek														
Observed 1936-45	Max	29.1	34.2	42.6	52.9	64.4	70.8	81.8	79.0	69.7	55.1	36.8	32.5	54.1
	Min	15.7	17.2	22.0	28.1	35.2	41.3	43.8	40.3	38.0	34.0	24.8	22.0	30.2
	Mean	22.4	25.7	32.3	40.5	49.8	56.1	62.8	59.7	53.9	44.6	30.8	27.3	42.2
Adj. to 50 yrs 1931-80	Max	28.8	35.1	41.1	50.9	63.4	71.5	80.6	78.2	68.8	53.0	36.8	31.1	53.3
	Min	16.4	19.8	22.1	27.7	34.9	41.5	43.2	41.4	37.5	32.8	25.4	21.2	30.3
	Mean	22.6	27.5	31.6	39.3	49.2	56.5	61.9	59.9	53.2	42.9	31.1	26.2	41.8
Burke (2 ENE) ¹														
	Max	28.7	34.6	39.7	48.0	58.8	67.2	77.1	75.0	65.1	52.5	36.8	31.2	51.2
	Min	17.1	20.2	22.5	28.0	32.9	39.6	44.8	43.7	38.7	32.1	25.0	20.4	30.4
	Mean	22.9	27.4	31.1	38.0	45.9	53.4	61.0	59.4	51.9	42.3	30.9	25.8	40.8
Coeur d'Alene														
	Max	34.4	40.5	47.9	58.9	68.9	75.6	86.0	85.3	75.3	60.9	44.4	37.3	59.6
	Min	21.1	24.0	27.8	34.0	41.2	47.8	52.3	51.1	44.5	37.4	30.1	26.1	36.5
	Mean	27.8	32.3	37.9	46.5	55.1	61.7	69.2	68.2	59.9	49.2	37.3	31.7	48.1
Kellogg ^{2,3}														
	Max	34.3	40.9	47.8	58.5	68.3	75.1	85.6	84.2	74.4	60.4	44.0	37.0	59.2
	Min	20.0	24.2	28.5	34.4	41.1	47.3	50.7	48.8	43.0	35.9	29.0	24.5	35.6
	Mean	27.2	32.6	38.2	46.5	54.7	61.2	68.2	66.5	58.7	48.2	36.5	30.8	47.4
Kingston Ranger Sta. ⁴														
	Max						75.0	84.4	83.7	74.8				
	Min						43.8	46.2	44.8	40.2				
	Mean						59.4	65.3	64.3	57.5				
Magee Ranger Sta. ⁵														
	Max						71.8	82.0	81.0	71.7				
	Min						40.5	41.0	39.0	35.7				
	Mean						56.2	61.5	60.0	53.7				
Priest River Exp. For.														
	Max	30.1	37.1	45.0	56.9	67.1	73.4	82.8	81.6	71.6	56.6	39.1	32.5	56.2
	Min	17.5	20.2	24.1	30.1	37.6	43.9	46.5	44.7	39.1	32.9	26.7	22.6	32.2
	Mean	23.8	28.7	34.6	43.5	52.4	58.7	64.7	63.2	55.4	44.8	32.9	27.6	44.2
St. Maries														
	Max	34.7	41.7	49.2	59.8	69.3	76.0	86.2	85.2	75.8	61.6	44.4	37.3	60.1
	Min	20.5	24.5	27.9	33.5	40.3	46.1	49.1	47.0	41.3	35.2	29.0	25.0	35.0
	Mean	27.6	33.1	38.6	46.7	54.8	61.1	67.7	66.1	58.6	48.4	36.7	31.2	47.6
Sandpoint														
	Max	31.5	37.7	45.2	57.0	66.6	72.9	81.9	80.7	70.6	56.9	41.3	34.6	56.4
	Min	19.6	23.0	27.2	33.8	40.3	46.0	48.4	46.8	41.3	34.5	28.4	24.2	34.5
	Mean	25.6	30.4	36.2	45.4	53.5	59.5	65.2	63.8	56.0	45.7	34.9	29.4	45.5
Wallace (2 NE), Woodland Park ³														
	Max	32.9	38.9	44.7	54.8	64.3	71.0	81.5	80.3	70.8	58.4	42.7	35.7	56.3
	Min	17.9	21.6	24.9	31.6	37.8	43.7	47.0	45.8	40.1	34.1	27.2	22.6	32.9
	Mean	25.4	30.3	34.8	43.2	51.1	57.4	64.3	63.1	55.5	46.3	35.0	29.2	44.6

¹Averages estimated from 1949-67 data.

²Averages adjusted for 4 or 5 years, 1966-70, when station was at airport (see text) and for 1 or 2 years missing data, 1973-74.

³Averages based on 24-hour period ending about 0800 or 0900 P.s.t.

⁴Averages estimated from 1951-70 data.

⁵Averages estimated from 1963-72 data.

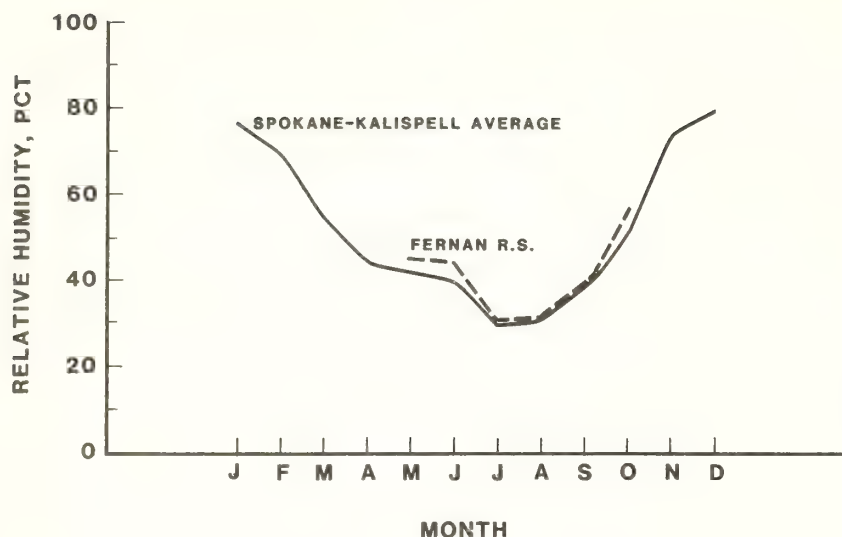


Figure 11—Annual pattern of afternoon relative humidity adjacent to Idaho panhandle area, shown by average of Spokane, WA, and Kalispell, MT, airport data at 1600 P.s.t. (1700 m.s.t.), based on 1960-82. Comparative May through October 1500 P.s.t. averages at Fernan Ranger Station based on 1951-80.

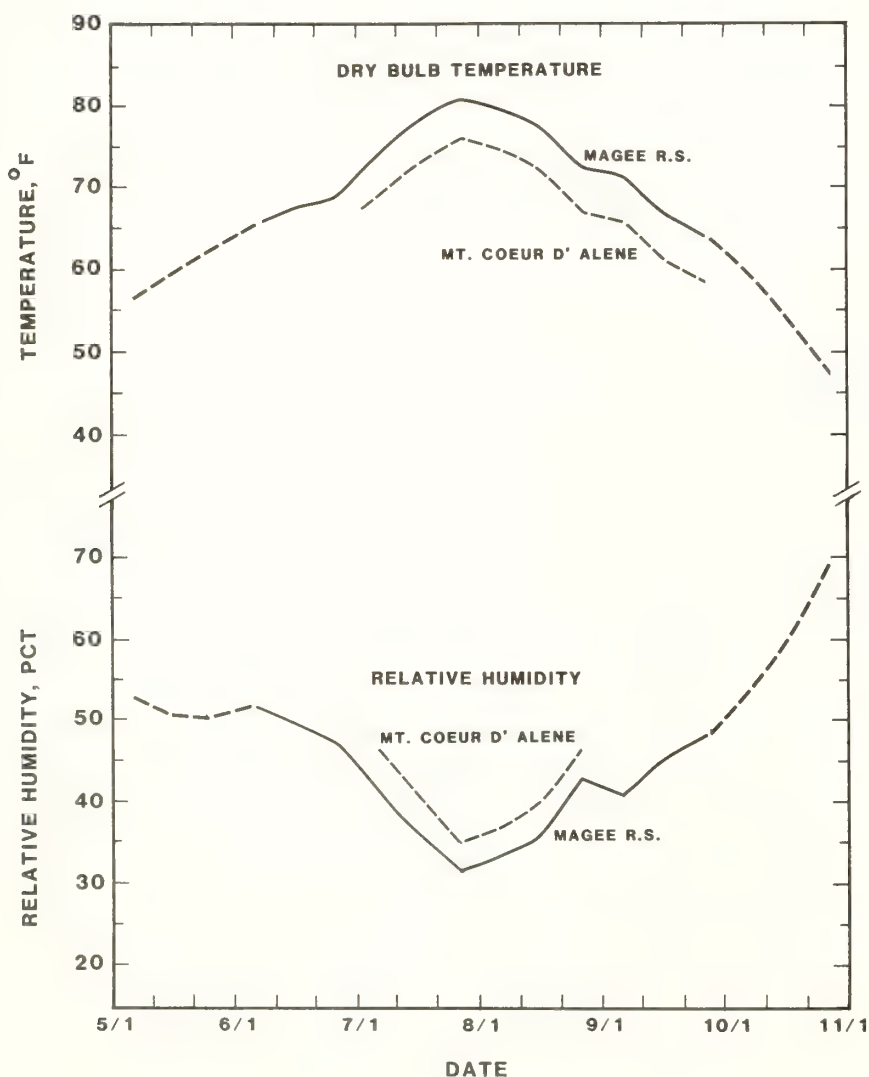


Figure 12—Average dry bulb temperature and relative humidity at 1500 P.s.t., by 10 (or 11)-day periods, plotted at middle of periods. Based on data adjusted to 30 years 1951-80 and adjusted for change in observation time to 1200 beginning in 1974. For Magee Ranger Station, elevation 3,000 ft, and Mount Coeur d'Alene Lookout, elevation 4,400 ft. Dashed portion of Magee curve denotes extrapolation based on data from Fernan Ranger Station and Kingston Ranger Station.

Annual Regime, Relative Humidity—The general yearly course of afternoon relative humidity is indicated in figure 11, with the aid of adjacent airport station data. Actual values at Deception Creek are most likely higher than those portrayed—they are definitely higher than those at Fernan Ranger Station during the fire season (as shown in a following section). The mid- or early-afternoon humidity at Deception Creek should average 80 percent or higher during the wet months of November, December, and January. This average decreases to about 50 to 55 percent in May and June, and to below 40 percent in July and August. Because of local shading and related radiational cooling (Schroeder and Buck 1970), however, fair-weather humidity values at headquarters typically exhibit a large rise by 1700 P.s.t. in August.

In the bottom area, relative humidity around dawn probably averages at least 90 to 95 percent throughout the year. This would be somewhat higher than the 4-year (1949-52) average values at 0400 P.s.t. shown for the Coeur d'Alene airport (Pacific Northwest River Basins Commission 1968), which range from 75 percent in July to 91 percent in December. Daily maximum humidity at Deception Creek headquarters, from a hygrothermograph of uncertain accuracy, averaged between 98 and 100 percent for the months May through October 1940-45.

Temperature and Relative Humidity During the Fire Season—Ten-day average midafternoon dry bulb temperature and relative humidity are portrayed in figure 12 for elevations near 3,000 ft and 4,500 ft. Interpolation may be made for intermediate elevations. In deriving the figure, adjusted 1963-72 averages from Magee Ranger Station were utilized rather than the data from Deception Creek headquarters. Magee was judged to be more broadly representative of a 3,000-ft location, as a starting point for interpolations, than is Deception Creek.

In figure 12, the largely temperature-dependent relative humidity (Schroeder and Buck 1970) follows almost a mirror image of the seasonal course of dry bulb temperature. Further, the relative humidity trend corresponds closely with that of average precipitation (fig. 7). For an open slope location at 4,000 ft, figure 12 gives estimated relative humidity averages ranging from about 55 percent in early June to 35 percent in late July and early August, to over 50 percent in late September. Midafternoon dry bulb averages peak at 77 to 78 °F.

Available station averages of summer afternoon dry bulb temperature and relative humidity are mapped in figure 13. Comparisons between the ranger stations and lookouts indicate an overall temperature lapse rate of about 4.0 °F per 1,000 ft. Relative humidity shows an elevational increase of 3.5 to 4.0 percent per 1,000 ft.

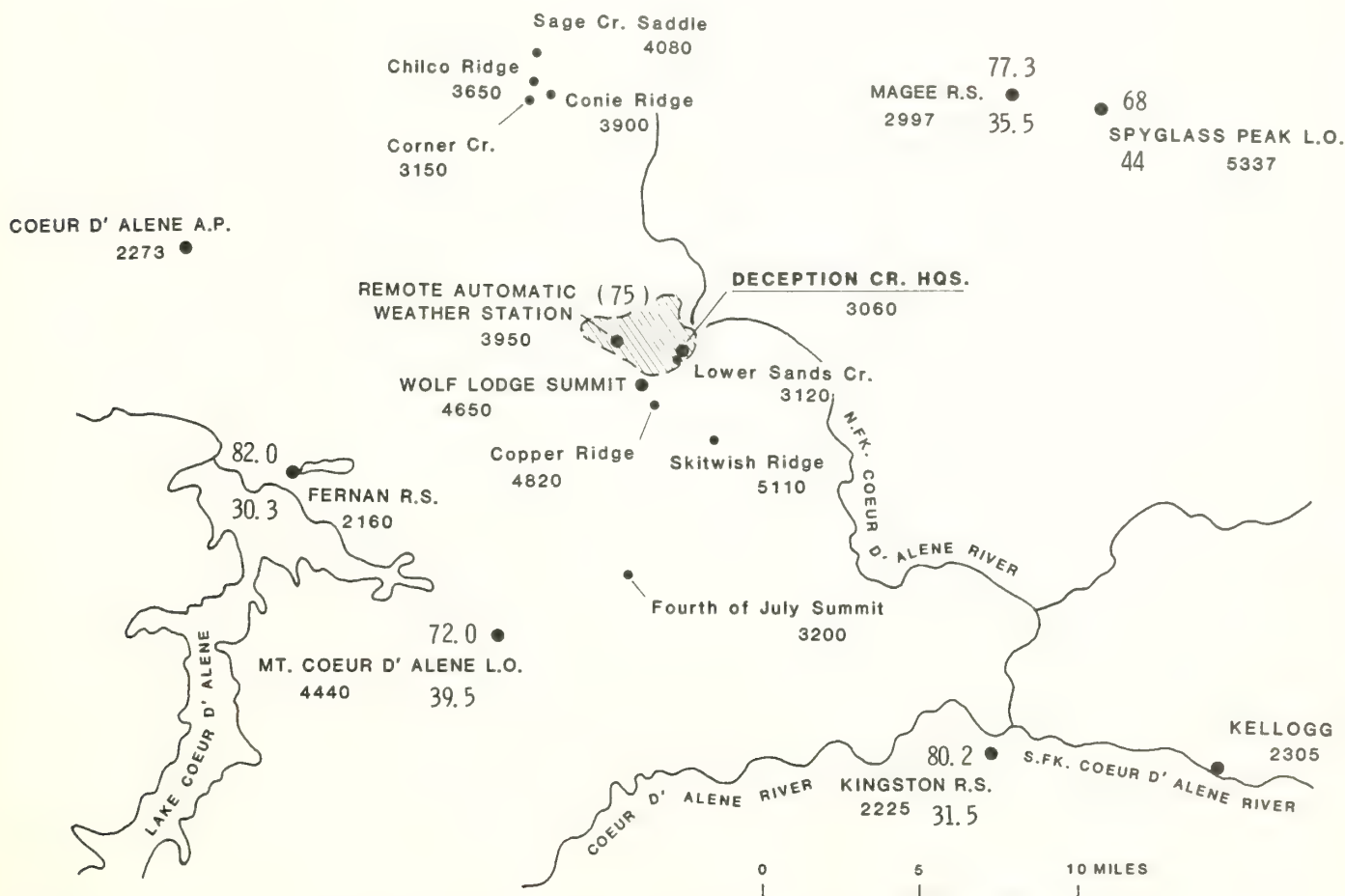


Figure 13—Average July-August dry bulb temperature, degrees Fahrenheit (top or only number) and relative humidity, percent (bottom number), at 1500 P.s.t.; based on or adjusted to 20 years 1951-70. Value in parentheses is an estimate based on 1 year.

Afternoon Shading Effects at Deception Creek—

Figure 14 portrays the cooling effect of afternoon shading at the sheltered Deception Creek headquarters site, and it indicates the difficulty in adjusting the original 1630 P.s.t. averages to those for midafternoon (1500). As the fire season progresses and shading occurs earlier, an increase is found in the average differences between the 1630 Deception Creek and Fernan dry bulb readings. During 1939-45 these differences increased from 6 °F in June to 9 or 10 °F in August, and to 12 °F in September. The average differences in maximum temperatures, occurring earlier in the day, held generally between 6 and 8 °F.

Average relative humidity at 1630 P.s.t. exhibits a more remarkable seasonal trend, with a large rise noted at headquarters. The Deception Creek-Fernan humidity difference (fig. 14) increased from about 8 percent in June to 20 percent in mid-August, and to 30 percent by mid-September. Daily-minimum relative humidity differences are smaller but, even so, averaged about 15 percent in September.

A similar tendency was found in a comparison of headquarters and RAWS data for 1984 (Finklin 1985). Daytime minimum relative humidity recorded at headquarters averaged 4 percent lower than the RAWS values during

July, 1 percent lower in August, and 3 percent higher in September. This minimum averaged 19 percent higher at headquarters than at RAWS during a 2-week period of fair weather from late September to October 10, with the excess reaching 30 to 40 percent on six of the days. Maximum temperatures at headquarters, compared with those at RAWS, averaged 3 °F higher during July and 1 °F higher in August, but 7 °F lower during the early-autumn spell of fair weather; they were 10 to 16 °F lower on five of these days. During cool, stormy periods of 4 or 5 days, both preceding and following this fair weather, headquarters maximum temperatures averaged 5 °F higher than those at RAWS.

In contrast to the Deception Creek-Fernan comparison, figure 14 shows that differences between Magee and Fernan at 1500 P.s.t. held fairly steady throughout the fire season. This was also found between RAWS and Fernan during 1984 in a comparison of 1200 or 1300 P.s.t. data.

An even earlier afternoon shading effect may have occurred at the Honeysuckle Ranger Station site. The 1933-35 data show that by 1700 P.s.t., the dry bulb temperature averaged 9 °F below the daily maximum temperature in July and 12 °F below the maximum in August.

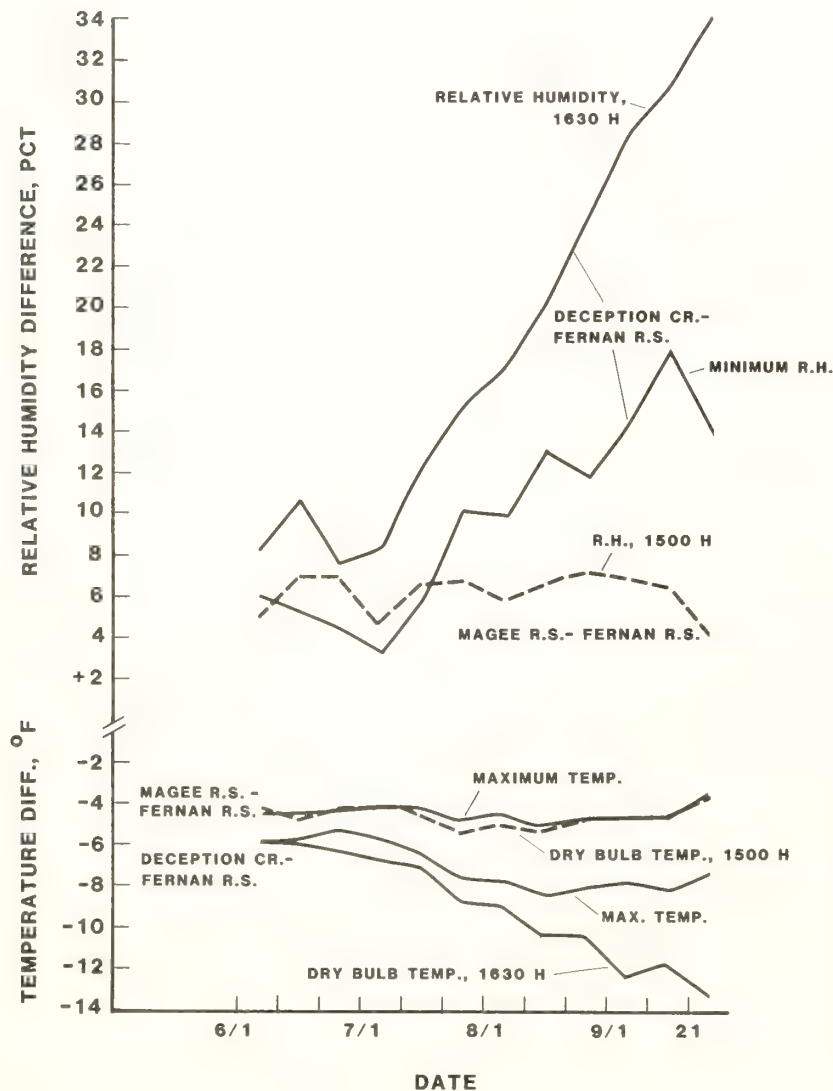


Figure 14—Differences in 10 (or 11)-day average temperatures, degrees Fahrenheit, and relative humidity (RH), between Deception Creek headquarters and Fernan Ranger Station; based on 5 to 7 years during 1939-45 (observations at 1630 P.s.t.), except minimum relative humidity is based on 2 or 3 years. Comparative differences between the Magee and Fernan Ranger Stations are based on mostly 10 years, 1963-72 (observations at 1500 P.s.t.).

Corresponding afternoon temperature decreases at Deception Creek during 1936-37 (before a change to 1630 P.s.t. observations in 1938) averaged just 6 °F in July and 9 °F in August; 13 °F in September.

Frequencies of Specific Values—The frequency or probability of specified midafternoon dry bulb and relative humidity values may be estimated from figure 15. Percentages shown, for the 3,000-ft and 4,500-ft locations, were adjusted from those observed during shorter periods of record. These adjustments were aided by the use of frequency-versus-average diagrams (Finklin 1983a).

Interpolating from figure 15, for an open slope location at 4,000 ft, the long-term frequency of midafternoon humidity less than 30 percent ranges from about 6 percent during May and early June to 50 percent in late July, falling to 10 percent in late September.

Summary Tables—Statistical summaries and frequencies of observed dry bulb temperature and relative humidity data (unadjusted) are given in tables 11 (appendix) and 12 (appendix), respectively. Where possible, the period 1951-70 has been used for the mainly 1500 P.s.t. observation

time. The summarized lookout data, limited to July and August, are subject to a bias, which gives too high an average dry bulb and too low an average relative humidity in both early July and late August (Finklin 1983a).

This results from an often shorter operational season for lookouts, and consequent missing data, in years with cool, moist (low fire danger) conditions.

Separate summaries for 1200 P.s.t. covering the 1974-84 period are presented for Fernan Ranger Station. A comparison shows generally lower average dry bulb and higher average relative humidity than during 1951-70, particularly in July and August. In these months, overall, the 1974-84 dry bulb averages 4 or 5 °F lower and the relative humidity averages 10 percent higher. A similar characteristic has been found by the senior author elsewhere in the northern Rocky Mountain area. About one-half of these differences may represent a generally cooler, moister regime in recent years, but the other half may be the effect of an earlier observation time. Caution is thus needed in interpreting the recent statistics for long-term and midafternoon application.

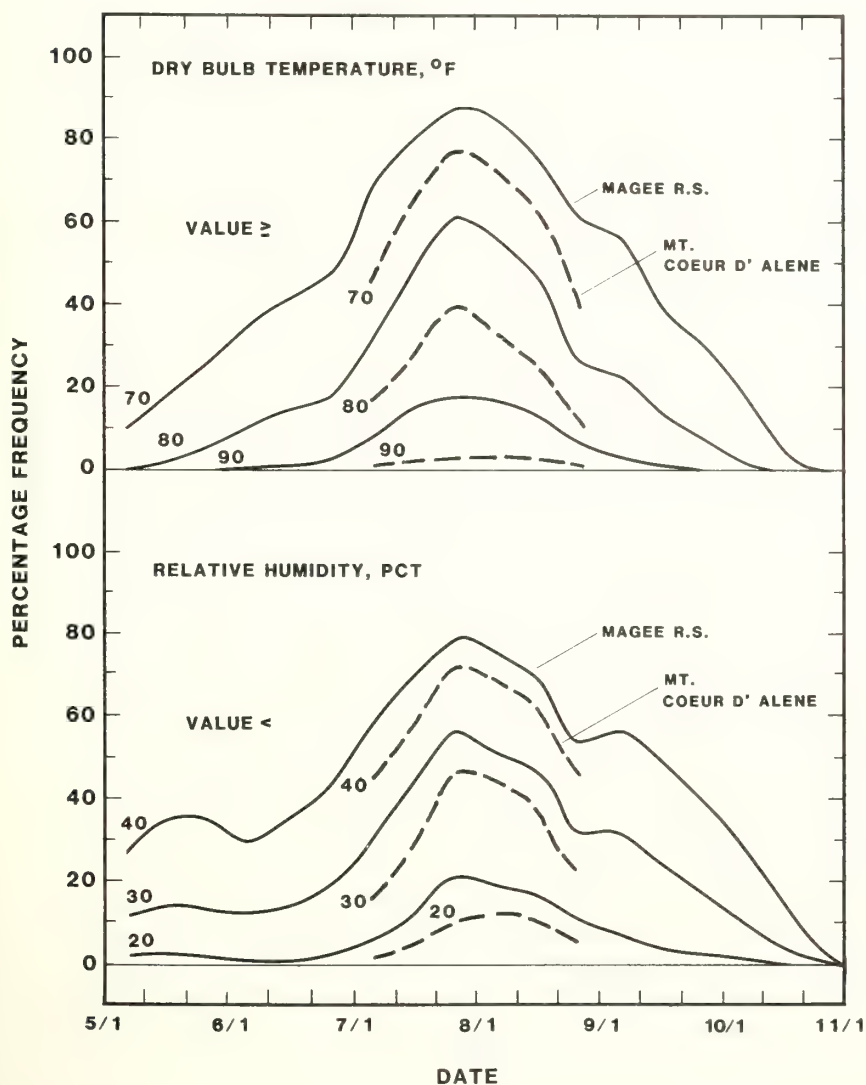


Figure 15—Frequencies of specified dry bulb temperature and relative humidity at 1500 P.s.t., by 10 (or 11)-day periods, plotted at middle of periods. Based on data adjusted to 30 years 1951-80 and relationship between average values and frequencies. For stations as in figure 12.

Diurnal Variation—The daily course of temperature and relative humidity at a slope location is depicted in figure 16. The curves, based on transmitted hourly RAWS data during 1984, apply to fair-weather days, when diurnal variations are of most interest to fire managers. Greater daily ranges and extremes can generally be expected at bottom locations, as shown for Priest River (Finklin 1983c). This was true at Deception Creek headquarters with respect to nighttime conditions in 1984, with headquarters cooler and more moist than RAWS. On the 32 July and August days represented in figure 16, headquarters minimum temperatures averaged 6 °F lower than those at RAWS and were as much as 12 °F lower. Maximum relative humidity at headquarters averaged 18 percent higher than at the RAWS site and was as much as 40 percent higher. As already noted, however, afternoon conditions were not consistently more extreme (warmer and drier) at headquarters than at RAWS, particularly in late season.

Figure 16 shows the shorter daytime period of low humidity in late season (past mid-September). The RAWS minimum relative humidity then occurs around 1400 P.s.t., compared with 1600 in July-August. The RAWS July and August temperatures at 1200, on fair days, average 2 °F lower than those at 1500, the former fire-weather observa-

tion time. Corresponding relative humidity averages 4 percent higher at the earlier hour.

Temperature Trends—Temperature trends or fluctuations during the past 70 years are indicated in figure 17. As calculated from the adjacent station data, the 5-year annual mean temperatures rose about 2 °F from the 1910's to 1936-40, when the mean peaked at 0.7 °F above the 1931-80 average. A subsequent decrease to about 0.9 °F below average occurred during 1946-50, followed by a rise to 0.4 °F above average during 1966-70 and a decrease to 0.7 °F below average most recently (during 1981-85). Little overall change is apparent, however, since the early 1930's. The 5-year means can, of course, smooth considerably the deviations that occur in individual years (table 8, appendix).

Graphs for the various seasons exhibit some greater fluctuations than those of annual temperature and, like those of seasonal precipitation (fig. 9), these may follow opposite directions. The 5-year means were relatively low for all seasons during the 1910's (and for autumn and winter through the 1920's), and they generally followed the 1936-40 peak, 1946-50 dip, and 1966-70 peak of the annual graph. A notable exception is the below-normal mean during winter 1936-40. Overall warming since the 1910's has amounted to 2 °F for May-June and apparently 3 °F

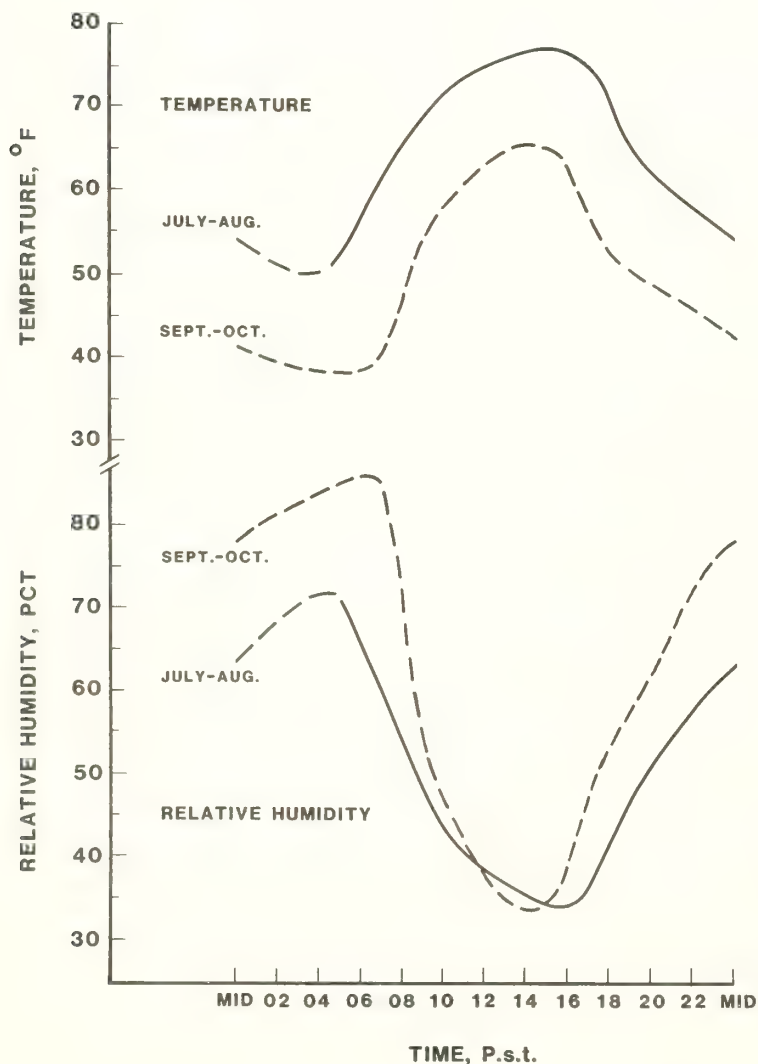


Figure 16—Average diurnal course of temperature and relative humidity on fair-weather days at Deception Creek RAWS site, 1984. July-August curves are based on 32 generally alternate days (16 each month); September-October curves (dashed line), on 10 available days between September 15 and October 10. Dashed portion of July-August curves is estimated due to missing data.

for July-August. Except for an upturn in winter, however, little long-term trend is suggested to date since 1930.

Wind

Throughout the year, the general wind over the Idaho panhandle, governed by large-scale air-pressure patterns (Schroeder and Buck 1970), is most often from the southwest or west. Significant variations in flow pattern can, of course, be expected between individual days and over longer periods. Windspeeds in the free atmosphere tend to be highest in winter and lowest in summer. Winds near the ground, influenced by topographic features and surface friction, may differ greatly with location and also with time of day.

Prevailing wind directions listed by the U.S. Weather Bureau (1936) are from the south every month of the year at Gibbs (Coeur d'Alene), southwest at Kellogg and Sandpoint, and mostly west at St. Maries. In the open prairie area at Coeur d'Alene airport, 6 years of data from all hours of the day (Pacific Northwest River Basins Commission 1968) show wind directions clustered mainly between southeast and west-southwest and between north and northeast. The monthly average (24-hour) windspeeds were all between 7 mi/h (during June through November) and 8 mi/h. An average of 1 to 2 mi/h was observed throughout the year (measured 8 ft above ground) at the sheltered Priest River headquarters (Finklin 1983c). Windspeed data for Deception Creek are limited to the fire season.

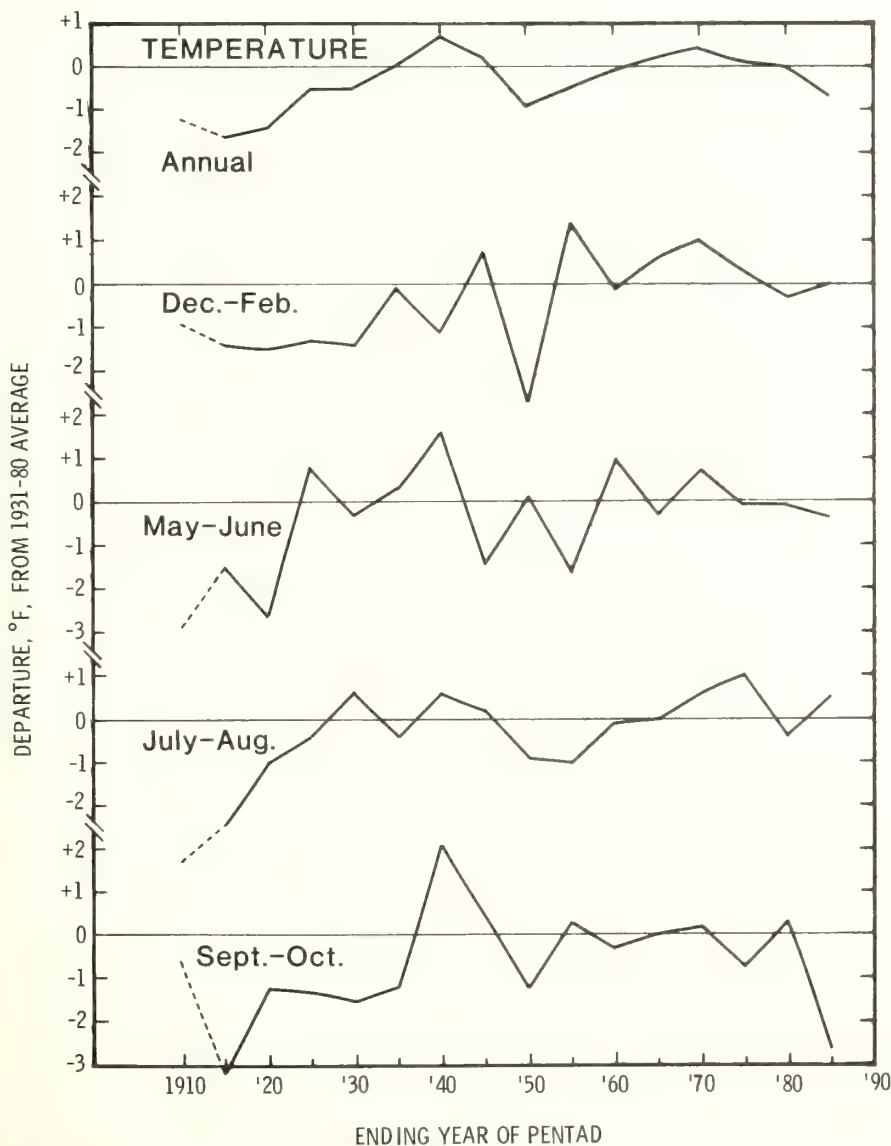


Figure 17—Fluctuations of annual and seasonal mean temperatures since 1910's in northern Idaho area adjacent to Deception Creek; shown by successive 5-year (pentad) averages, plotted as in figure 9. Values are based on arithmetic averages of maximum and minimum temperatures and are given as departures, degrees Fahrenheit, from 50-year, 1931-80, averages. Calculated by weighted averaging of departures obtained at each of five stations as in figure 9, except formula employed was $\frac{1}{4}(A + B + C + \frac{1}{2}[D + E])$. Adjustment was made for Kellogg 1966-70 data (see text) and three outliers were discarded (Coeur d'Alene departure for winter 1926-30 and St. Maries departures for winters 1976-80 and 1981-85).

Wind During the Fire Season—Summer afternoon wind conditions observed in the Deception Creek-Coeur d'Alene National Forest area are portrayed in figure 18. Prevailing wind directions are mainly from the southwest or west but do show local topographic channeling effects. The mid-afternoon speeds average mostly 5 or 6 mi/h, even at the two lookouts, Mount Coeur d'Alene and Spyglass Peak. The 3 mi/h afternoon average at Deception Creek headquarters is a noticeable exception (the 1630 P.s.t. average here was slightly less, about 2.5 mi/h). Winds were also light at the former Honeysuckle Ranger Station, with a July-August 1933-35 average speed of 2.0 to 2.5 mi/h at 1700 and about 3.5 mi/h for the afternoon (1200-1700 average). The RAWS data for 1984-85 show the early afternoon wind prevailing from the northwest during July and August, with an average speed of 5 mi/h.

The 24-hour average windspeed at headquarters, measured during 1936-39, was 1.4 mi/h in July and 1.3 mi/h in August, decreasing from 1.7 mi/h in May to 0.8 mi/h in October. The 24-hour average at Honeysuckle Ranger Station during 1933-35 was 2.4 mi/h in July and 2.2 mi/h in August.

Detailed afternoon windspeed and direction frequencies are given in table 13 (appendix). The speeds represent mostly a 10-minute average at the observation time. At the two lookout stations, these speeds are found to exceed 12 mi/h on only 2 to 4 percent of the days during July-August. Such frequencies would, of course, be greater if shorter durations and all times of day or afternoon were considered.

For example, Deception Creek RAWS data for 26 days during July and August 1985 show that 10-minute windspeeds for both 1300 and 1500 P.s.t. averaged 5 mi/h. Peak gusts during the preceding 1-hour periods averaged 14.5 mi/h.

Downslope and downcanyon airflows, or drainage breezes, may be expected during fair-weather nighttime hours. The 1984-85 data indicate such wind is usually very light at the north-slope RAWS site. Average July-August windspeeds were 2 mi/h at 2100 P.s.t., and 1 to 1.5 mi/h at 0000 (midnight) and 0300. The wind most frequently was from a downslope direction (south through west-southwest). On nights with such a direction, during 1985, past-hour peak gusts averaged 7 mi/h at 2100 and 5 mi/h at the two later times.

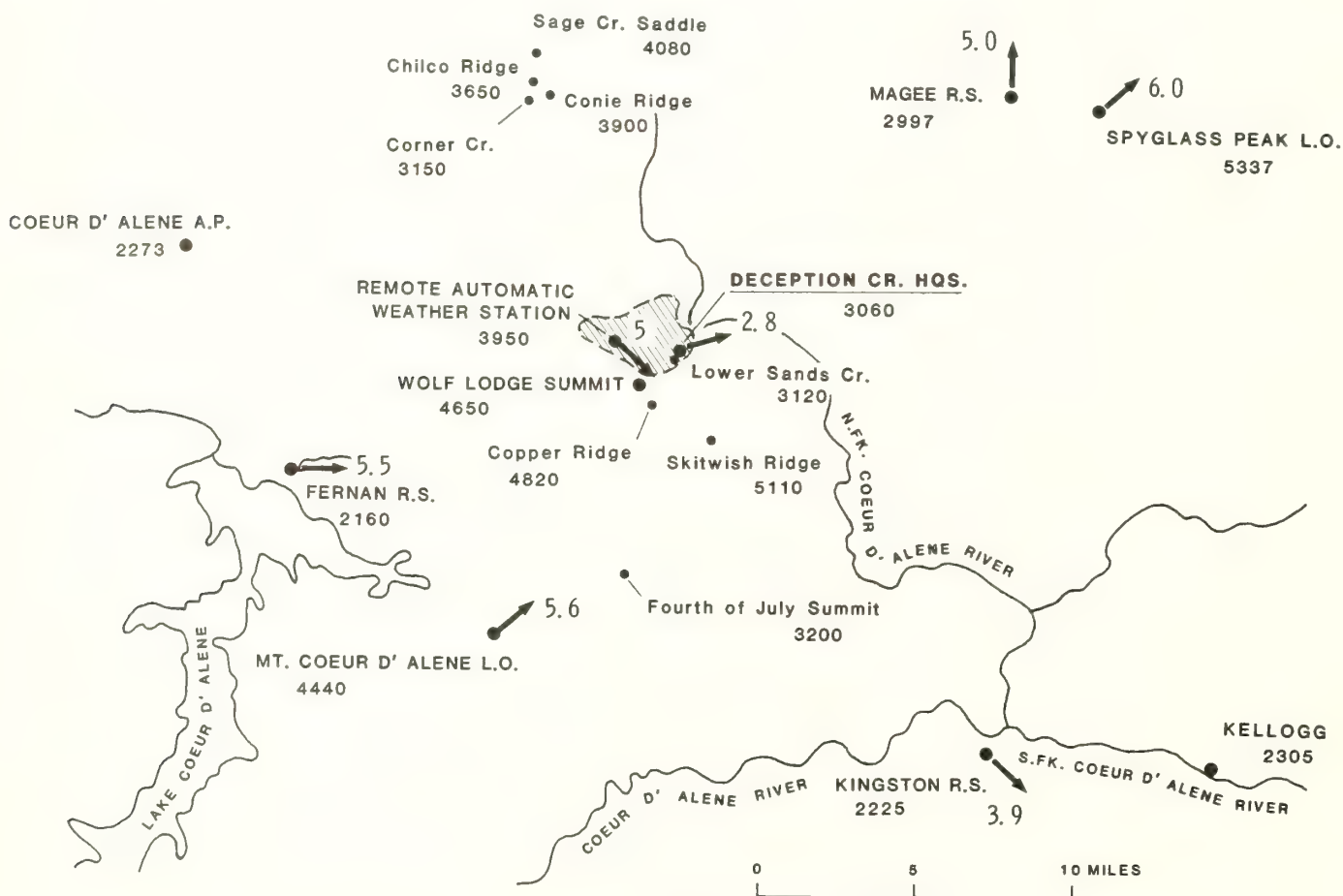


Figure 18—Prevailing wind direction (arrow points downwind) and average speed, miles per hour, in midafternoon (mostly about 1500 P.s.t.), July and August. Based on period 1954-70, except 1963-72 at Magee Ranger Station; 1936-45 direction at 1630 P.s.t. and 1936-42 "afternoon average" speed at Deception Creek headquarters; 1984-85 data at Remote Automatic Weather Station.

Combined Frequencies of Temperature, Humidity, and Windspeed

Observed three-way frequencies during the fire season for 1500 P.s.t. conditions are presented in table 14 (appendix). Again, these are based on varying and relatively short periods of record, making only monthly frequencies appropriate. Application will require summation by the user to obtain frequencies for broader ranges of temperature, humidity, and windspeed, as well as for frequencies of values above or below certain thresholds. Interpolation between stations and months may be helpful—for example, interpolation between ranger stations and lookouts for estimates at open slope locations. Variations may be expected between differing slope aspects (Geiger 1965; Barry 1981), but no further guidance can be offered here.

REFERENCES

- Barry, Roger G. Mountain weather and climate. London; New York: Methuen; 1981. 313 p.
- Bradshaw, Larry S.; Fischer, William C. Computer programs for summarizing climatic data stored in the National Fire Weather Data Library. General Technical Report INT-164. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1984. 39 p.
- Brown, Merle J.; Peck, Eugene L. Reliability of precipitation measurements as related exposure. *Journal of Applied Meteorology*. 1(2): 203-207; 1962.
- Cooper, Stephen V.; Neiman, Kenneth; Steele, Robert. Forest habitat types of northern Idaho: a second approximation. General Technical Report. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; [in press].
- Deeming, John E.; Burgan, Robert E.; Cohen, Jack D. The National Fire-Danger Rating System—1978. General Technical Report INT-39. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 63 p.
- Finklin, Arnold I. Summarizing weather and climatic data—a guide for wildland managers. General Technical Report INT-148. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983a. 43 p.
- Finklin, Arnold I. Weather and climate of the Selway-Bitterroot Wilderness. Moscow, ID: University Press of Idaho; 1983b. 144 p.
- Finklin, Arnold I. Climate of Priest River Experimental Forest, northern Idaho. General Technical Report INT-159. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983c. 53 p.
- Finklin, Arnold I. Weather summary for Deception Creek, Idaho, area, fire season 1984. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory; 1985; Office Report. 17 p.
- Finklin, Arnold I. A climatic handbook for Glacier National Park—with data for Waterton Lakes National Park. General Technical Report INT-204. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 124 p.
- Furman, R. William; Brink, Glen E. The National Fire Weather Data Library. General Technical Report RM-19. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1975. 8 p.
- Geiger, Rudolf. The climate near the ground. Rev. ed. Cambridge, MA: Harvard University Press; 1965. 611 p.
- Landsberg, Helmut. Physical climatology, 2d ed. DuBois, PA: Gray Printing; 1958. 446 p.
- Linsley, Ray K.; Kohler, Max A.; Paulhus, Joseph L. H. Hydrology for engineers. New York: McGraw-Hill; 1958. 340 p.
- MacHattie, L. B.; Schnelle, F. An introduction to agrotopoclimatology. Technical Note No. 133. WMO-No. 378. Geneva: World Meteorological Organization; 1974. 131 p.
- National Oceanic and Atmospheric Administration, Environmental Data Service. Monthly normals of temperature, precipitation, and heating and cooling degree days 1951-80. *Climatology of the United States* No. 81 (by State). Idaho section. Asheville, NC: National Climatic Center; 1982.
- Pacific Northwest River Basins Commission, Meteorology Committee. Climatological handbook, Columbia Basin States, 3 vol. Vancouver, WA: Pacific Northwest River Basins Commission; 1968. 540 p., 262 p., 641 p., plus appendices.
- Schroeder, Mark J.; Buck, Charles C. Fire weather. *Agriculture Handbook* 360. Washington, DC: U.S. Department of Agriculture; 1970. 229 p.
- U.S. Department of Agriculture, Soil Conservation Service; Idaho Department of Water Resources. Summary of snow survey measurements in Idaho, 1921-79. Portland, OR: U.S. Department of Agriculture, Soil Conservation Service; ca. 1980. 393 p.
- U.S. Weather Bureau. Climatic summary of the United States [Bulletin W, 1930 ed.]. Section 5—northern Idaho. Washington, DC: U.S. Department of Agriculture; 1936. 15 p.
- U.S. Weather Bureau. Climatic summary of the United States—supplement for 1931 through 1952. *Climatology of the United States* No. 11-8, Idaho. Washington, DC: U.S. Department of Commerce; 1958a. 46 p.
- U.S. Weather Bureau. Substation history, Idaho. Key to meteorological records documentation No. 1.1. Washington, DC: U.S. Department of Commerce; 1958b. 63 p.
- Wellner, C. A.; Foiles, M. W. What to see and where to find it on the Deception Creek Experimental Forest. Miscellaneous Publication 2. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Rocky Mountain Forest and Range Experiment Station; 1951. 72 p.
- World Meteorological Organization. A note on climatological normals. Technical Note No. 84. WMO-No. 208.TP.108. Geneva: World Meteorological Organization; 1967. 15 p.

APPENDIX: TABLES 5-14

Table 5--Monthly and annual precipitation, inches, by individual years; at Deception Creek headquarters (data limited to 1936-45), Coeur d'Alene, and Kellogg, ID. T denotes trace, an amount too small to measure. M denotes amount missing, no estimate made. E denotes amount estimated in whole or part, different from originally published value or estimate; F is correction using fire-weather data; P, estimate as published

Deception Creek Headquarters

Year	Precipitation												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
	Inches												
1936	M	M	M	M	2.45	4.13	0.92	0.72	1.84	1.15	.31	11.49	M
1937	4.46	7.95	3.49	8.54	1.70	6.02	1.25	2.12	1.74	3.96	14.02	9.70	64.95
1938	5.91	4.26	6.73	5.58	1.69	1.91	.33	1.04	1.16	4.58	5.96	6.61	45.76
1939	8.50	8.95	4.81	1.29	1.10	4.06	.85	.04	1.93	3.91	2.13	11.51	49.08
1940	3.19	11.21	7.58	6.05	1.88	1.18	1.28	.24	4.21	6.01	6.60	8.09	57.52
1941	5.37	1.94	2.37	1.09	8.46	3.30	.24	1.63	5.35	3.36	5.60	9.85	48.56
1942	1.93	4.53	5.02	4.95	5.67	4.88	1.43	.33	.28	7.89	11.44	5.59	53.94
1943	4.87	5.40	5.61	5.79	4.41	3.30	.52	.83	.34	6.41	3.30	7.93	48.71
1944	2.86	2.66	2.17	3.69	4.14	1.53	.92	2.08	3.91	1.97	6.25	4.51	36.69
1945	9.17	5.33	10.28	3.69	3.71	2.21	.00	1.06	8.41	8.40	9.69	7.17P	69.12

(con.)

Table 5 (Con.)

Coeur d'Alene

Year	Precipitation												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
----- Inches -----													
1914	5.14	3.02	1.33	2.33	1.32	1.49	1.71	0.25	2.31	2.17	2.24	1.39	24.70
1915	1.40	2.38	1.32	1.68	3.55	1.61	1.26	.00	1.20	.64	4.11	3.60	22.75
1916	3.48	2.20	5.37	1.94	1.90	3.20	1.21	.95	1.07	.39	4.00	2.52	28.23
1917	2.69	2.26	2.79	3.24	3.06	1.08	.00	.00	.42	.44	1.33	6.65	23.96
1918	2.74	3.05	2.24	.30	1.46	.37	.42	.88	1.56	2.52	2.29	1.92	19.75
1919	3.61	6.09	2.94	1.67	1.30	.59	.00	1.13	.77	.98	1.28	1.12	21.48
1920	2.25E	.50	2.52	2.26	2.12	1.00	.50	2.07	3.29	1.68	2.05	3.67	23.91
1921	4.35	2.52	2.80	2.21	.77	1.35	.22	1.25	.46	1.75	4.23	2.12	24.03
1922	1.99	1.70	2.23	2.64	.28	.09	.38	1.18	.71	1.78	.77	5.11	18.86
1923	4.15	1.52	1.39	1.60	1.33	3.43	.98	1.78	.13	1.62	2.27	3.99	24.19
1924	3.21	2.12	1.00	.38	.41	.62	.90	1.29	1.48	2.82	4.27	2.54	21.04
1925 ¹	4.87	3.14	1.80	1.22	2.45	1.35	.12	.40	1.09	.90	1.89	3.48	22.71
1926	3.50	3.47	.62	.85	1.43	1.88	.22	3.66	2.06	1.52	4.15	2.60	25.96
1927	2.84	4.43	1.87	1.64	2.92	2.14	.56	.44	6.29	3.08	5.41	3.93	35.55
1928	2.95	.21	3.51	1.60	1.15	1.35	1.18	.04	.11	.86	2.37	3.37	18.70
1929	1.55	.74	1.56	2.58	1.02	2.09	.01	.20	.43	.78	.05	4.17	15.18
1930	.95	2.31	1.48	1.74	2.37	1.89	.11	.07	1.06	1.18	3.00	1.33	17.49
1931	2.48	1.92	2.93	1.71	.64	.95	T	T	1.46	1.93	4.69	5.93	24.64
1932	3.08	2.56	4.47	2.88	4.55	.38	.55	.16	.24	2.35	4.45	4.21	29.88
1933	3.59	1.72	2.44	.70	1.43	1.69	.17	.70	2.16	3.66	1.36	9.91	29.53
1934	4.41	.42	3.87	1.20	.91	2.50	.11	.06	1.35	4.63	3.57	4.09	27.12
1935	5.21	1.20	2.44	1.18	.50	.75	.52	1.47	.25	.77	1.73	2.97	18.99
1936	5.39	2.21	1.72	.49	.82	2.82	.65	.11	1.19	.52	.15	4.05	20.12
1937	3.14	4.34	1.47	4.41	.41	3.63	1.03	1.20	.82	1.21	4.95	5.16	31.77
1938	2.46	2.95	3.26	1.60	.84	1.79	.43	.49	.62	1.10	2.01	2.98	20.53
1939 ²	2.93	3.24	1.51	.71	1.17	1.50	.50	.12	.78	2.06	.77	5.20	20.49
1940	2.01	6.49	3.58	2.74	.92	.45	1.43	.11	4.62	3.84	3.99	3.35	33.53
1941	2.53	1.35	.65	.32	4.54	2.17	.03	1.34	2.41	1.39	2.79	5.06	24.58
1942	1.53	2.56	.88	1.74	4.74	2.57	.53	.16	.04	2.31	6.21	3.33	26.60
1943	3.12	2.87	2.46	2.30	1.06	1.93	.40	.44	.25	3.78	1.04	1.61	21.26
1944	1.73	1.66	1.33	2.09	1.30	1.90	.44	1.69	1.75	.70	2.52	2.24	19.35
1945	2.88	2.19	4.66	1.61	3.57	1.53	T	.44	3.52	1.58	5.76	3.35	31.09
1946	3.96	2.96	3.17	1.88	1.52	1.39	.22	.05	1.50	2.57	5.47	1.98	26.67
1947	3.00	.44	2.41	1.52	1.02	5.00	.38	.90	3.10	6.30	2.28	2.63	28.98
1948	3.88	3.71	1.26	3.42	6.16	3.37	3.69	.32	.66	1.20	3.78	3.93	35.38
1949	.73	5.44	1.91	.80	1.37	.46	.62	.83	2.35	1.98	3.24	3.57	23.30
1950	4.73	2.82	4.40	1.06	1.04	2.98	1.14	.95	.38	4.48	2.25	2.63	28.86
1951	4.38	2.07	2.86	.44	1.28	1.88	.86	.68	.71	6.96	2.49	6.39	31.00
1952	3.67	1.54	1.28	.88	.88	2.25	.32	.53F	.52	.35	.68	4.00	16.90
1953	5.32	1.91	1.91	2.12	2.29	1.66	T	1.22	.38	.52	3.73	3.13	24.19
1954	6.82	1.61	.86	1.20	1.36	1.58	1.30	2.83	1.30	1.43	2.45	2.80	25.54
1955 ³	1.50	2.16	.94	2.54	1.33	1.82	1.86	T	1.54	4.12	5.03	5.25	28.09
1956	4.51	2.11	2.44	.47	2.83	2.60	1.16	1.81	1.01	3.60	.95	2.72	26.21
1957 ³	2.09	2.83	2.61	1.48	6.43	2.63	.09	.49	.86	3.22	1.64	3.08	27.45
1958	4.15	3.63	1.33	3.94	.63	2.13	1.13	.25	.71	2.11	6.30	4.57	30.88
1959	5.45	2.36	2.03	1.65	2.06	.79	.11	.65	2.81	2.53	3.79	1.65	25.88
1960	1.94	2.22	3.12	2.19	3.72	.82	T	2.17	1.13	1.70	5.99	1.43	26.43

(con.)

Table 5 (Con.)

Coeur d'Alene (Con.)

Year	Precipitation												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
	----- Inches -----												
1961	2.35	5.67	2.78	1.47	2.22	1.05	.36	.62	.35	1.53	2.07	4.44	24.91
1962	2.27	1.47	4.13	.89	2.35	.73	.28	1.03	1.04	2.73	3.42	3.10	23.44
1963	.55	3.71	1.39	1.75	1.67	1.66	1.03	.63	1.36	1.45	4.59	2.91	22.70
1964	4.25	.53P	2.71	1.19	.58	4.01	1.49	2.63	1.65	1.05	2.91	7.85	30.85
1965	3.73	2.14	.15	3.02	1.27	2.36	.22	3.54	1.04	.26	2.29	1.79	21.81
1966	4.07	.92	4.32	.35	.63	1.47	.55	.59	.21	.82	5.19	3.63	22.75
1967	4.84	1.05	2.04	2.34	2.18	2.03	.04	T	.70	3.26	1.89	2.74	23.11
1968	2.81	4.16	.95	.48	2.41	2.01	.35	2.32	2.29	3.49	3.46	3.78	28.51
1969	8.23	1.37	.74	2.67	1.51	2.30	.32	.00	1.35	1.37	.54	3.46	23.86
1970	8.23	3.27	2.12	2.24	.81F	1.87	1.10	.32	.89	2.63	3.47	4.17	31.12
1971	4.01	1.77	2.98	1.99	2.11	4.62	.88	1.90	2.05	1.82	2.64	4.95	31.72
1972	4.37	3.13P	2.79	2.32	2.33	1.61	.67	1.64	1.21	.83	1.72	3.41P	26.03
1973	2.96	.95	1.69	.95	1.48	.99	.00	.16	2.10	1.14	8.76	5.42	26.60
1974	7.54	2.84	3.24	1.76	1.82	.76	1.56	.75	.54	.06	3.59	3.21	27.67
1975	4.50	3.95	2.43	2.00	1.31	1.77	1.78	2.14	T	3.50	2.60	3.97	29.95
1976	2.74	3.82	1.83	1.76	1.75	2.36	.65	2.28	.00	.58	.89	1.39	20.05
1977	1.46	.65	1.67	.23	3.04	1.14	1.08	1.00	2.32	.84	2.67	6.73	22.83
1978	3.21	2.16	2.12	2.02	3.98	1.05	2.15	3.32	1.44	.15	2.01	2.44	26.05
1979	2.13	3.70	1.75	1.58	1.37	1.31	.62	1.34	.52	1.81	1.32	2.18	19.63
1980	2.45	2.19	1.77	1.64	4.75	3.34	.30	.92	1.25	.99	2.64	5.87	28.11
1981	1.60	3.28	1.60	2.79	2.41	3.97	.80	.21	1.37	2.49	2.31	4.33	27.16
1982	4.00	4.56	2.73	3.53	.79	.48	1.73	.27	1.79	2.79	3.61	4.70	30.98
1983	2.65	2.91	4.72	.74	1.32	3.94	3.22	1.64	.84	1.94	6.46	3.69	34.07
1984	2.51	2.19	2.59	2.30	3.15	3.04	.20	.23	1.42	2.02	5.66	5.18	30.49
1985	.39	2.01	2.09	.79	2.26	1.43	.00	2.49	2.56	1.05	3.21	.78	19.06
10-year averages													
1921-30	3.04	2.22	1.83	1.65	1.41	1.62	.47	1.03	1.38	1.63	2.84	3.26	22.37
1931-40	3.47	2.71	2.77	1.76	1.22	1.65	.54	.44	1.35	2.21	2.77	4.79	25.66
1941-50	2.81	2.60	2.31	1.67	2.63	2.33	.75	.71	1.60	2.63	3.53	3.03	26.61
1951-60	3.98	2.24	1.94	1.69	2.28	1.82	.68	1.06	1.10	2.65	3.31	3.50	26.26
1961-70	4.13	2.43	2.13	1.64	1.56	1.95	.57	1.17	1.09	1.86	2.98	3.79	25.31
1971-80	3.54	2.52	2.23	1.63	2.39	1.90	.97	1.55	1.14	1.17	2.88	3.96	25.86
30-year averages													
1921-50	3.11	2.51	2.30	1.69	1.75	1.87	.59	.73	1.44	2.16	3.05	3.69	24.88
1951-80	3.88	2.40	2.10	1.65	2.08	1.89	.74	1.26	1.11	1.90	3.06	3.75	25.81
50-year average													
1931-80	3.58	2.50	2.28	1.68	2.02	1.93	.70	.99	1.25	2.10	3.10	3.81	25.94

(con.)

Table 5 (Con.)

Kellogg

Year	Precipitation												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
	Inches												
1905	M	M	2.58	1.23	3.43	3.15	0.57	0.48	2.03	5.95	3.04	1.78	M
1906	2.84	2.92	1.46	.90	5.86	2.49	.12	1.01	.70	2.23	5.95	5.44	31.92
1907	3.88	3.30	3.43	1.80	1.30	1.91	.64	2.23	1.53	.56	2.18	2.99	25.75
1908	2.72	2.55	4.22	1.72	2.88	2.02	.47	.64	1.15	4.00	1.65E	2.77	26.79
1909	6.68	3.40	1.36	1.28	1.71	1.33	2.95	.23	2.65	1.51	7.88	1.65	32.63
1910	2.93	4.43	2.41	2.80	2.70	.61	.06	.00	1.25	3.97	5.20	2.27	28.63
1911	2.77	2.39	1.36	1.37	5.29	2.79	.60	1.48	1.72	1.17	5.00	1.68	27.62
1912	3.81	3.21	1.69	2.79	4.26	2.64	1.40	2.29	2.80	2.91	4.15	3.00	34.95
1913	6.69	1.09	3.87	1.74	2.61	4.55	1.75	1.19	1.23	2.81	3.47	.43	31.43
1914	4.45	3.10	2.35	2.55	1.50	2.04	.60	.30	2.22	3.00	4.41	1.67	28.19
1915	1.29	2.40	2.55	1.99	5.44	1.75	2.26	.58	1.60	2.04	4.68	4.14	30.72
1916	2.64	3.01	6.75	2.67	2.21	3.62	3.28	2.39	3.22	.54	3.82	3.05	37.20
1917	3.82	2.50	3.10	3.25	2.83	1.88	.05	T	2.62	1.25	1.08	12.03	34.41
1918	5.18	3.75	2.83	.92	2.66	.77	.92	1.19	.93	4.53	2.45	.81	26.94
1919	3.54	4.10	3.19	2.47	2.41	.70	.35	.47	1.17	2.22	3.33	2.16	26.11
1920	3.74	.21	4.74	2.65	3.24	2.08	2.62	1.61	4.00	3.10	2.82	3.44	34.25
1921	3.33	2.85	5.07	3.63	.92	1.21	.37	1.18	1.34	2.76	4.70	3.66	31.02
1922	2.17	1.90	1.87	2.18	.67	.34	.74	1.91	1.13	1.92	.73	4.39	19.95
1923	5.12	.75	2.62	2.53	1.93	3.83	.90	2.22	.28	1.69	4.27	4.21	30.35
1924	3.08	3.25	1.44	1.27	.14	1.14	.78	.89	1.51	2.24	5.18	4.13	25.05
1925	6.42	4.16	3.51	1.87	3.15	2.24	.73	1.50	.88	1.35	2.06	2.98	30.85
1926	2.95	3.66	.91	1.20	2.44	1.30	.62	3.66	2.99	3.12	6.18	3.93	32.96
1927	4.05	4.94	2.70	1.43	3.23	2.46	.75	.25	5.94	4.74	7.51	3.82	41.82
1928	3.95	.61	5.13	3.00	1.39	1.27	.31	.00	.15	1.85	2.73	2.53	22.92
1929	2.41	1.83	2.78	1.80	.67	2.82	.00	.25	.65	1.74	.08	6.10	21.13
1930	1.16	3.00	2.25	2.97	4.27	1.53	.49	.21	.72	2.08	3.41	1.75	23.84
1931	2.32	1.81	3.27	3.42	.94	2.05	1.17	.18	2.30	2.53	4.34	3.37	27.70
1932	2.86	3.47	5.23	1.90	3.49	1.03	.64	.62	.26	3.55	7.27	3.74	34.06
1933	4.48	2.88	2.62	.75	2.04	2.89	.80	.50	2.65	6.60	2.62	12.28	41.11
1934	4.86	.51	5.06	1.41	2.36	1.85	.12	.00	2.28	5.31	3.25	3.02	30.03
1935	4.51	1.00	4.93	2.47	.38	1.39	.55	.70	.41	1.92	1.43	2.49	22.18
1936	5.13	3.88	2.61	1.03	1.70	3.16	.64	.59	.96	.63	.34	4.73	25.40
1937	2.53	3.92	1.94	5.64	1.22	2.39	.77	2.16	1.15	2.28	4.86	4.77	33.63
1938	2.99	2.35	4.38	2.79	.91	1.70	.08	.65	1.80	2.90	2.56	2.89	25.91
1939	2.83	3.67	2.13	.68	1.13	2.44	.60	.00	.89	1.96	1.27	5.89	23.49
1940	2.56	5.76	3.20	3.00	1.56	.81	1.23	.08	2.54	3.16	5.12	2.63	31.65
1941	1.79	.97	1.07	.90	5.93	2.53	.28	1.27	3.78	3.10	3.11	4.33	29.06
1942	1.68	2.45	1.32	2.28	5.26	3.93	1.49	.53	.15	2.80	6.62	2.75	31.26
1943	2.55	1.80	2.77	3.37	2.73	2.93	.51	.82	.35	4.05	.89	2.76	25.53
1944	1.42	1.66	1.55	2.08	1.00	1.35	.35	.68	2.65	.88	2.99	3.26	19.87
1945	4.04	2.32	4.29	3.47	2.17	1.68	.00	.51	4.84	2.91	4.55	3.52	34.30
1946	3.61	2.51	3.26	1.96	1.70	2.89	.69	.36	1.62	3.26	7.93	3.71	33.50
1947	3.57	2.86	3.64	2.08	1.49	3.93	.30	.89	2.31	6.10	4.57	2.85	34.59
1948	4.61	3.55	2.55	5.02	4.48	4.50	4.12	.73	.80	1.34	4.47	4.06	40.23
1949	1.45	5.20	2.45	1.66	1.71	1.00	.79	.97	1.84	2.47	4.12	5.47	29.13
1950	6.28	4.75	5.34	2.06	1.54	2.95	1.36	1.17	.99	7.23	3.20	3.96	40.83
1951	3.43	4.23	2.30	.62	3.61	1.99	.89	.71	1.23	6.82	3.82	4.98	34.63
1952	2.94	1.60	1.87	1.09	2.48	3.59	.02	.46	.85	.20	.50	3.48	19.08
1953	8.48	2.73	2.03	2.92	3.52	2.48	.00	1.21	.53	.82	4.24	4.18	33.14
1954	7.29	2.41	1.69	3.12	2.18	2.87	1.84	2.93	2.73	1.96	3.26	1.81	34.09
1955	1.63	2.05	2.69	3.15	1.56	2.51	1.73	T	2.74	6.14	5.28	6.33	35.81
1956	3.87	3.10	3.89	.82	2.87	2.63	1.66	2.09	1.34	3.57	.96	3.50	30.30
1957	2.75	5.28	3.41	2.37	5.08	2.16	.66	.74	.32	3.13	1.64	3.80	31.34
1958	3.41	4.42	1.35	4.01	.99	3.28	1.38	.57	1.62	1.79	6.23	5.93	34.98
1959	6.11	1.50	2.78	2.29	2.62	2.02	.32	.78	4.20	3.51	4.96	1.64	32.73
1960	2.27	2.84	3.42	3.16	3.76	1.67	.01	1.92	.75	2.52	5.04	2.20	29.56

(con.)

Table 5 (Con.)

Kellogg (Con.)

Year	Precipitation												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
	----- Inches -----												
1961 ⁴	2.45	7.34	2.80	2.82	4.00	1.31	.14	.68	1.40	2.33	2.74	4.34	32.35
1962	3.41	1.66	3.72	1.90	3.59	.72	1.09	1.27	1.94	3.14	3.55	3.09	29.08
1963	1.18	3.70	3.21	2.84	1.10	2.66	1.23	.23	1.33	1.67	2.87	2.72	24.74
1964	4.27	1.16	3.02	2.27	1.04	3.66	1.97	2.68	1.94	1.94	3.44	6.53	33.92
1965 ⁵	5.08	2.80	.71	3.73	1.40	2.38	.42	3.28	1.93	.75	2.64	1.67	26.79
1966	4.51	1.90	3.21	.83	.70	2.85	.56	1.02	.26	1.23	5.82	4.09	26.98
1967	5.09	2.02	1.78	1.35	1.60E	1.70E	.19	.04	1.11	3.48	2.04	2.45	22.85
1968	2.21	5.24	1.46	1.24	1.75	2.58	.33	1.98	3.79	3.47	3.03	4.80	31.88
1969	7.69	.87	1.59	2.39	1.45	1.60	.42	.07	2.04	1.98	1.17	3.71	24.98
1970 ⁶	6.35	2.12	2.67	3.23	1.55E	3.07	1.62	.90	1.72	2.24	2.85E	2.67E	31.00
1971	5.91	2.34	3.22	2.78	2.69	3.89	.55	2.09	2.33P	1.93	1.98	4.67	34.38
1972	4.34	4.67	3.90	2.70	2.48	2.43	1.01	.80	1.66	.65	1.32	4.09P	30.05
1973	3.70	.94	1.82	.85E	.83E	.92	.00	.34	2.60E	1.20E	8.45E	5.80E	27.45
1974 ⁷	9.30E	4.10E	3.85E	2.80E	2.35E	1.30E	1.10E	.55E	.70E	.10E	4.25E	3.35E	33.75E
1975 ⁷	5.10E	4.22	3.18	1.80	1.51	1.82	1.30	2.85	.10	3.54	3.25	5.75	34.42
1976	3.71	3.55	2.26	2.35	1.85	1.66	.73	2.99	.12	1.20	2.08	2.03	24.53
1977	1.75	1.48	2.49	.43	3.15	1.67	1.73	1.38	3.21	1.49	3.24	8.16	30.18
1978	3.19	2.14	2.03	2.38	4.29	1.26	2.04	2.97	1.96	.48	2.37	3.59	28.70
1979	2.12	4.56	2.14	2.59	2.23	.38	1.65	1.19	.60	2.17	1.33	4.16	25.12
1980	3.92	1.86	1.94	1.58	4.99	4.74	1.17	1.32	2.88	.89	2.88	7.17	35.34
1981	1.53	2.71	1.77	3.88	3.08	4.93	1.08	.55	1.53	2.35	3.82	4.97	32.20
1982	6.33	5.48	3.83	4.07	1.44	1.61	2.38	1.06	1.92	3.07	4.79	3.74	39.72
1983	3.54	2.92	3.75	1.46	2.31	3.87	3.29	1.18	1.21	1.72	6.57	4.15	35.97
1984	4.14	1.86	3.54	2.74	5.09	2.96	.16	.23	3.33	3.03	4.77	4.35	36.20
1985	.57	1.82	2.11	1.20	2.29	2.22	T	2.41	4.11	3.00	5.18	1.12	26.03
10-year averages													
1911-20	3.79	2.58	3.24	2.24	3.25	2.28	1.38	1.15	2.15	2.36	3.52	3.24	31.18
1921-30	3.46	2.70	2.83	2.19	1.88	1.81	.57	1.21	1.56	2.35	3.69	3.75	27.99
1931-40	3.51	2.93	3.54	2.30	1.57	1.97	.66	.55	1.52	3.08	3.31	4.58	29.52
1941-50	3.10	2.81	2.82	2.49	2.80	2.77	.99	.79	1.93	3.41	4.25	3.67	31.83
1951-60	4.22	3.02	2.54	2.36	2.87	2.52	.85	1.14	1.63	3.05	3.59	3.79	31.57
1961-70	4.22	2.88	2.42	2.26	1.82	2.25	.80	1.22	1.75	2.22	3.02	3.61	28.46
1961-70 ⁸	4.62	3.00	2.58	2.48	1.98	2.30	.83	1.23	1.77	2.30	3.02	3.72	29.83
1971-80	4.30	2.99	2.68	2.03	2.64	2.01	1.13	1.65	1.62	1.37	3.12	4.88	30.39
30-year averages													
1921-50	3.36	2.81	3.06	2.33	2.09	2.18	.74	.85	1.67	2.95	3.75	4.00	29.78
1951-80	4.38	3.00	2.60	2.29	2.49	2.28	.94	1.34	1.67	2.24	3.24	4.13	30.60
(Adj.)													
50-year average													
1931-80	3.95	2.95	2.83	2.33	2.37	2.31	.89	1.07	1.70	2.64	3.46	4.13	30.63
(Adj.)													

¹Station moved to Gibbs, at lumber company near west edge of Coeur d'Alene, in September 1925.²Station moved to Fernan Ranger Station in May 1939.³Equipment moved 0.2 miles south-southeast in September 1955, 350 ft north-northwest in Sept. 1957.⁴Equipment, at mining company, moved 500 ft west in April 1961.⁵Station moved 3 mi west-northwest to Shoshone County Airport in December 1965.⁶Station moved back to Kellogg in May 1970, observations discontinued in September 1973.⁷Station reestablished, at water power company, in February 1975.⁸Adjusted for apparently lower amounts at airport location.

Table 6--Precipitation statistics for Deception Creek headquarters as observed during 1936-45; for Coeur d'Alene, 50 years 1931-80. Number 0.00 denotes either zero or trace. Year (YR), first two digits omitted, is the most recent in cases of more than one occurrence

P R E C I P I T A T I O N													
BY 10 (OR 11)-DAY AND MONTHLY PERIODS													
STATION DECEPTION CREEK HQ YRS 1936-1945													
PERIOD BEGINS	NO. YRS	MEAN TOTAL	10-DAY AND MONTHLY TOTALS				LOWEST TOT, YR	I	MAXIMUM DAILY TOTALS				
			STD. DEV	MEDIAN	HIGHEST TOT.	YR			EXTREME YR	AVE MAX	STD DEV	MEDIAN	
MAY 1	9	1.200	0.952	1.180	3.12	41	0.00	39	I 1.00 36	0.548	0.333	0.560	
MAY 11	9	1.264	1.397	0.760	4.31	41	0.16	44	I 2.08 41	0.618	0.607	0.550	
MAY 21	10	1.169	1.255	0.730	3.38	44	0.04	36	I 2.20 44	0.728	0.769	0.495	
JUN 1	10	1.248	0.974	0.955	3.76	36	0.40	38	I 1.48 36	0.624	0.342	0.485	
JUN 11	10	1.373	1.120	1.300	3.88	37	0.03	40	I 1.37 37	0.599	0.433	0.535	
JUN 21	10	0.607	0.599	0.480	1.64	42	0.00	40	I 0.77 41	0.354	0.305	0.355	
JUL 1	10	0.264	0.331	0.120	0.84	36	0.00	45	I 0.76 39	0.178	0.257	0.055	
JUL 11	10	0.278	0.478	0.065	1.35	42	0.00	45	I 0.65 42	0.151	0.227	0.060	
JUL 21	10	0.232	0.410	0.025	1.17	40	0.00	45	I 0.79 40	0.160	0.275	0.025	
AUG 1	10	0.222	0.436	0.020	1.36	37	0.00	39	I 0.69 37	0.137	0.232	0.020	
AUG 11	10	0.256	0.389	0.065	1.00	38	0.00	43	I 0.66 44	0.143	0.215	0.055	
AUG 21	10	0.531	0.403	0.600	1.41	41	0.04	39	I 0.77 41	0.427	0.280	0.570	
SEP 1	10	1.157	0.936	0.890	2.55M	45	0.03	42	I 2.17 40	0.794	0.751	0.560	
SEP 11	9	0.994	1.049	0.910	2.81	41	0.00	38	I 1.30 44	0.499	0.460	0.630	
SEP 21	9	0.316	0.422	0.070	1.20	44	0.00	43	I 0.63 44	0.207	0.238	0.060	
OCT 1	9	0.961	0.434	0.940	1.62	41	0.41	36	I 0.76 39	0.553	0.162	0.490	
OCT 11	9	1.327	1.162	1.200	3.29	43	0.00	44	I 1.84 38	0.817	0.642	0.740	
OCT 21	9	2.101	2.236	1.360	6.92	42	0.00	36	I 4.17 42	1.023	1.249	0.840	
MONTH									I				
MAY	9	3.758	2.287	3.710	8.46	41	1.10	39	I 2.20 44	1.196	0.680	1.000	
JUN	10	3.228	1.547	3.300	6.02	37	1.18	40	I 1.48 36	0.892	0.323	0.765	
JUL	10	0.774	0.484	0.885	1.43	42	0.00	45	I 0.79 40	0.420	0.280	0.475	
AUG	10	1.009	0.736	0.935	2.12	37	0.04	39	I 0.77 41	0.466	0.259	0.580	
SEP	9	2.312	1.774	1.920	5.32	41	0.28	42	I 2.17 40	0.888	0.673	0.830	
OCT	9	4.389	2.144	4.060	7.89	42	1.15	36	I 4.17 42	1.477	1.081	1.260	

(con.)

Table 6 (Con.)

STATION NUMBER			101956	COVER D'ALENE				YRS 1931-1980						
PERIOD BEGINS	NO. YRS	MEAN TOTAL	10-DAY AND MONTHLY TOTALS						MAXIMUM DAILY TOTALS					
			STD. DEV	MEDIAN	HIGHEST TOT, YR	LOWEST TOT, YR	I I	EXTREME YR	AVE MAX	STD DEV	MEDIAN			
JAN 1	49	1.060	0.805	0.960	3.76	48	0.05	38	I	1.28	66	0.477	0.324	0.410
JAN 11	49	1.279	1.018	1.290	5.19	74	0.00	48	I	1.67	72	0.511	0.385	0.510
JAN 21	49	1.136	0.928	0.860	4.00	70	0.00	80	I	2.19	54	0.532	0.432	0.460
FEB 1	50	0.942	0.767	0.845	3.17	49	0.00	76	I	1.77	49	0.434	0.368	0.385
FEB 11	50	0.849	0.800	0.600	3.26	61	0.00	77	I	1.63	70	0.384	0.331	0.310
FEB 21	50	0.708	0.677	0.575	3.39	40	0.00	70	I	1.06	57	0.352	0.283	0.285
MAR 1	50	0.747	0.624	0.615	2.80	66	0.00	68	I	0.95	66	0.335	0.238	0.300
MAR 11	50	0.727	0.580	0.610	2.39	45	0.00	34	I	1.50	72	0.335	0.262	0.305
MAR 21	50	0.802	0.651	0.590	2.72	62	0.00	39	I	1.55	62	0.384	0.298	0.315
APR 1	50	0.515	0.464	0.390	1.83	58	0.00	66	I	1.32	58	0.263	0.252	0.220
APR 11	50	0.564	0.496	0.430	2.12	55	0.00	62	I	0.81	44	0.315	0.234	0.305
APR 21	50	0.599	0.462	0.490	1.90	53	0.00	73	I	1.05	53	0.348	0.266	0.305
MAY 1	50	0.601	0.554	0.480	2.14	48	0.00	71	I	0.97	48	0.278	0.237	0.290
MAY 11	50	0.672	0.872	0.455	5.22	57	0.00	79	I	1.70	57	0.345	0.341	0.255
MAY 21	50	0.737	0.773	0.575	3.21	32	0.00	63	I	2.04	32	0.372	0.398	0.270
JUN 1	50	0.813	0.759	0.645	3.61	47	0.00	65	I	1.81	64	0.440	0.379	0.385
JUN 11	50	0.645	0.647	0.425	2.57	37	0.00	63	I	1.17	43	0.370	0.370	0.210
JUN 21	50	0.469	0.500	0.300	1.78	55	0.00	79	I	1.29	58	0.290	0.316	0.215
JUL 1	50	0.326	0.422	0.190	1.90	78	0.00	77	I	1.12	78	0.227	0.278	0.130
JUL 11	50	0.198	0.291	0.035	1.29	75	0.00	73	I	0.87	70	0.144	0.198	0.035
JUL 21	50	0.179	0.340	0.010	1.70	48	0.00	80	I	1.32	48	0.127	0.262	0.010
AUG 1	50	0.175	0.251	0.050	0.86	64	0.00	79	I	0.78	65	0.130	0.191	0.030
AUG 11	50	0.332	0.605	0.030	3.02	78	0.00	73	I	1.10	54	0.188	0.298	0.030
AUG 21	50	0.470	0.474	0.295	1.67	75	0.00	74	I	0.85	50	0.276	0.239	0.225
SEP 1	50	0.390	0.456	0.235	2.07	40	0.00	76	I	1.96	40	0.260	0.348	0.175
SEP 11	50	0.479	0.544	0.255	2.00	49	0.00	79	I	1.35	45	0.310	0.346	0.175
SEP 21	50	0.386	0.431	0.220	1.36	77	0.00	79	I	0.82	73	0.220	0.225	0.130
OCT 1	50	0.578	0.683	0.315	2.45	51	0.00	80	I	1.22	47	0.303	0.321	0.190
OCT 11	50	0.584	0.700	0.245	2.57	68	0.00	78	I	1.49	58	0.326	0.365	0.170
OCT 21	50	0.941	0.864	0.655	3.86	34	0.00	65	I	1.17	51	0.385	0.288	0.350
NOV 1	50	0.886	0.700	0.775	3.05	58	0.00	52	I	1.30	58	0.447	0.274	0.415
NOV 11	50	1.112	0.905	0.925	3.30	73	0.00	43	I	1.88	60	0.498	0.413	0.355
NOV 21	50	1.097	0.851	1.015	3.49	45	0.00	56	I	1.60	59	0.536	0.407	0.455
DEC 1	50	1.190	0.804	1.090	3.53	33	0.02	32	I	1.50	33	0.526	0.356	0.455
DEC 11	50	1.168	0.973	0.940	5.45	33	0.00	76	I	1.87	33	0.514	0.412	0.445
DEC 21	50	1.454	0.970	1.455	5.36	64	0.06	53	I	1.52	64	0.543	0.304	0.500
MONTH									I					
									I					
JAN	49	3.474	1.551	3.140	7.54	74	0.55	63	I	2.19	54	0.848	0.383	0.760
FEB	50	2.499	1.326	2.200	6.49	40	0.42	34	I	1.77	49	0.665	0.357	0.625
MAR	50	2.276	1.084	2.120	4.66	45	0.15	65	I	1.55	62	0.559	0.288	0.495
APR	50	1.678	0.923	1.640	4.41	37	0.23	77	I	1.32	58	0.526	0.249	0.495
MAY	50	2.011	1.471	1.455	6.43	57	0.41	37	I	2.04	32	0.595	0.388	0.495
JUN	50	1.927	1.025	1.805	5.00	47	0.38	32	I	1.81	64	0.709	0.359	0.645
JUL	50	0.702	0.692	0.525	3.69	48	0.00	73	I	1.32	48	0.362	0.313	0.290
AUG	50	0.977	0.918	0.690	3.54	65	0.00	69	I	1.10	54	0.390	0.284	0.390
SEP	50	1.255	0.959	1.085	4.62	40	0.00	76	I	1.96	40	0.507	0.358	0.440
OCT	50	2.104	1.530	1.750	6.96	51	0.06	74	I	1.49	58	0.622	0.328	0.625
NOV	50	3.095	1.782	2.655	8.76	73	0.15	36	I	1.88	60	0.776	0.394	0.705
DEC	50	3.813	1.671	3.435	9.91	33	1.39	76	I	1.87	33	0.809	0.355	0.715

Table 7--Observed frequencies of daily precipitation amounts at stations as in table 6

PRECIPITATION - PERCENT FREQUENCY OF DAILY AMOUNTS (INCHES)																
- GIVEN TO NEAREST TENTH PERCENT, DECIMAL POINT OMITTED																
STATION		DECEPTION CREEK HQ													1936-1945	
PERIOD BEGINS	TOTAL NUM. DAYS	TR	.01	.05	.10	.20	.30	.40	.50	.60	.80	1.00	1.50	2.00	3.00	4.00
MAY 1	88	125	409	318	295	216	170	159	114	57	23	11				
MAY 11	90	100	433	356	267	178	144	122	78	67	22	11	11	11		
MAY 21	110	118	336	236	182	109	91	91	73	64	36	36	18	9		
JUN 1	100	130	460	320	260	210	150	110	80	60	30	20				
JUN 11	100	50	510	390	280	220	150	130	110	90	40	20				
JUN 21	99	71	232	192	162	131	81	61	30	30						
JUL 1	100	20	180	110	70	40	30	20	10	10						
JUL 11	100	70	170	120	70	40	40	40	10	10						
JUL 21	110	36	100	73	45	36	27	18	18	9						
AUG 1	100	70	120	80	60	40	30	20	10	10						
AUG 11	100	40	170	120	80	50	20	10	10	10						
AUG 21	110	91	200	118	109	82	55	55	55	36						
SEP 1	98	51	316	286	265	122	92	82	82	61	31	31	31	10		
SEP 11	90	78	378	278	211	133	111	78	78	78	44	22				
SEP 21	90	56	167	111	67	56	56	33	22	11						
OCT 1	90	78	333	289	244	189	156	100	67	44						
OCT 11	90	11	367	311	244	156	111	111	78	78	56	44	22			
OCT 21	99	111	414	333	283	242	182	141	131	121	61	30	20	20	10	10
MONTH																
MAY	288	115	389	299	243	163	132	122	87	63	28	21	10	7		
JUN	299	84	401	301	234	187	127	100	74	60	23	13				
JUL	310	42	148	100	61	39	32	26	13	10						
AUG	310	68	165	106	84	58	35	29	26	19						
SEP	278	61	288	227	183	104	86	65	61	50	25	18	11	4		
OCT	279	68	373	312	258	197	151	118	93	82	39	25	14	7	4	4

(con.)

Table 7 (Con.)

PRECIPITATION - PERCENT FREQUENCY OF DAILY AMOUNTS (INCHES)

- GIVEN TO NEAREST TENTH PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		101956	COUER D'ALENE												1931-1980	
PERIOD BEGINS	TOTAL NUM. DAYS	TR	.01	.05	.10	AMOUNT EQUAL TO OR GREATER THAN										
						.20	.30	.40	.50	.60	.80	1.00	1.50	2.00	3.00	4.00
JAN 1	490		490	398	302	180	122	78	59	41	20	8				
JAN 11	490		508	414	337	220	147	114	82	53	20	12	2			
JAN 21	539		432	345	267	180	111	80	58	43	24	11	4	2		
FEB 1	500		422	352	276	168	100	66	44	36	16	10	2			
FEB 11	500		382	302	230	162	102	56	44	28	16	6	2			
FEB 21	413		421	337	264	150	99	63	39	27	15	7				
MAR 1	500		400	300	240	154	84	42	26	18	10					
MAR 11	500		408	324	248	134	80	42	22	6	6	2				
MAR 21	550		382	293	224	122	71	49	36	25	5	5	2			
APR 1	500		328	242	180	94	44	24	12	12	2	2				
APR 11	500		318	228	162	104	64	44	26	14	4					
APR 21	500		318	230	172	110	70	44	26	16	6	2				
MAY 1	500		378	262	182	120	72	38	14	8	2					
MAY 11	500		320	238	182	118	70	42	32	24	12	8	4			
MAY 21	550		340	251	175	100	75	53	40	24	11	5	2	2		
JUN 1	500		360	282	200	136	96	64	40	34	18	8	2			
JUN 11	500		308	240	166	94	62	48	38	28	20	12				
JUN 21	500		248	176	126	80	50	36	24	12	8	4				
JUL 1	500		186	122	78	54	38	26	14	12	4	2				
JUL 11	500		122	76	58	40	22	16	6	2	2					
JUL 21	550		91	69	55	22	13	5	5	5	4					
AUG 1	500		116	78	60	30	24	8	6	4						
AUG 11	500		134	104	78	54	44	36	20	14	10	4				
AUG 21	550		222	169	133	84	53	38	15	11	2					
SEP 1	500		198	148	110	68	40	30	18	14	6	2	2			
SEP 11	500		222	156	122	76	54	38	30	20	14	6				
SEP 21	500		224	168	118	76	48	26	10	6	4					
OCT 1	500		250	184	158	104	72	50	32	20	12	6				
OCT 11	500		276	196	148	90	68	44	34	26	18	4				
OCT 21	550		389	313	247	162	109	69	45	36	9	2				
NOV 1	500		404	326	234	162	104	74	50	36	12	4				
NOV 11	500		432	350	280	200	136	88	66	52	24	12	2			
NOV 21	500		402	330	280	200	142	82	62	40	22	18	4			
DEC 1	499		467	389	319	220	144	96	60	44	26	14	2			
DEC 11	500		466	382	310	216	144	84	56	36	16	14	4			
DEC 21	550		529	455	358	242	176	109	75	51	20	9	2			
MONTH																
JAN	1519		475	384	301	193	126	90	66	45	22	11	2	1		
FEB	1413		408	330	256	161	100	62	42	30	16	8	1			
MAR	1550		396	305	237	136	78	45	28	17	7	3	1			
APR	1500		321	233	178	103	61	37	21	14	4	1				
MAY	1550		346	250	179	112	72	45	29	19	8	5	2	1		
JUN	1500		305	233	164	103	69	49	34	25	15	8	1			
JUL	1550		132	88	63	38	24	15	8	6	4	2				
AUG	1550		159	119	92	57	41	28	14	10	4	1				
SEP	1500		215	157	117	73	47	31	19	13	8	3	1			
OCT	1550		308	234	186	120	84	55	37	28	13	4				
NOV	1500		413	335	265	187	127	81	59	43	19	11	2			
DEC	1549		489	410	330	227	156	97	64	44	21	12	3			

Table 8--Monthly and annual mean temperatures, degrees Fahrenheit, by individual years; at Deception Creek headquarters (data limited to 1936-45), Coeur d'Alene, and Kellogg, ID. Means are arithmetic averages of daily maximum and minimum values; based on 24-hour periods ending at indicated observation times (P.s.t.). E denotes mean is different from originally published value, includes estimates for missing days. Values in parentheses, at Kellogg, are completely estimated. M denotes data missing, no estimate made

Deception Creek Headquarters - Observation time 1630 P.s.t.

	Mean temperature												
Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
	°F												
1936	23.5	9.0	27.4	36.9	53.3	58.8	63.2	59.9	51.4	44.2	27.0	28.8	40.3
1937	5.6	22.5	33.4	37.9	47.5	56.4	62.8	56.9	54.0	46.0	34.4	28.8	40.5
1938	24.8	28.9	32.9	40.0	48.2	58.2	63.4	57.4	58.5	43.9	24.3	25.5	42.2
1939	28.1	20.1	32.0	40.1	49.5	52.7	62.3	60.6	53.6	43.0	33.5	30.9	42.2
1940	23.5	31.9	37.1	43.2	53.0	59.2	63.1	60.3	58.4	47.2	28.1	27.5	44.4
1941	27.8	30.9	38.4	45.9	49.9	57.7	65.5	61.1	49.5	42.6	34.9	28.5	44.4
1942	20.9	27.8	33.3	42.1	48.5	53.6	62.8	61.3	54.0	43.7	30.9	29.1	42.3
1943	18.8	28.8	25.5	40.5	46.9	51.9	60.8	58.3	53.6	46.1	32.0	23.0	40.5
1944	22.8	27.6	29.9	41.2	51.0	57.2	62.0	59.0	55.4	46.4	32.9	23.2	42.4
1945	28.2	30.2	33.0	37.2	50.2	54.6	62.8	61.9	50.1	44.2	30.4E	M	M

Table 8 (Con.)

Coeur d'Alene - Observation time mostly about 1700 m.s.t.; about 0800 during 1925-40 and 1400 to 1500 beginning in 1975

	Mean temperature												
Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
	°F												
1921	30.8	32.6	38.5	43.3	54.8	62.8	65.0	65.4	51.2	48.2	36.0	27.2	46.3
1922	21.1	23.6	33.8	42.5	52.5	65.2	68.2	67.0	58.9	48.8	33.0	22.6	44.8
1923	31.6	23.4	36.8	46.0	53.0	59.6	69.2	66.0	59.3	47.9	38.5	31.8	46.9
1924	23.4	38.5	37.8	45.8	59.2	59.4	66.6	63.5	57.8	47.4	35.1	23.5	46.5
1925 ¹	31.6	38.2	40.0	49.9	58.8	63.9	71.2	65.6	59.6	45.0	36.8	35.9	49.7
1926	30.0	37.4	42.5	52.2	55.3	63.4	73.0	66.2	52.4	49.0	39.2	29.5	49.2
1927	26.4	33.0	38.2	44.7	50.8	62.4	68.4	68.0	55.5	49.2	37.4	20.2	46.2
1928	27.2	29.4	40.2	43.8	59.0	61.6	71.4	67.2	59.3	47.7	35.8	27.9	47.5
1929	15.6	19.2	38.8	43.0	54.2	60.8	67.8	71.6	56.4	48.9	33.3	35.1	45.4
1930	13.9	36.2	39.3	51.4	52.6	59.2	70.9	70.6	60.2	44.8	35.6	28.0	46.9
1931	33.0	33.4	39.0	46.6	57.9	62.4	70.4	69.1	58.8	47.4	32.1	27.4	48.2
1932	25.0	26.7	34.4	46.4	53.2	63.7	66.7	67.4	58.4	47.2	40.8	24.8	46.2
1933	29.4	20.6	36.2	44.7	49.8	62.0	69.3	68.1	54.8	49.4	39.7	36.4	46.7
1934	36.0	36.5	44.6	54.2	58.8	63.2	68.8	69.8	56.0	49.1	42.2	32.6	51.0
1935	28.0	32.5	35.6	42.4	53.6	60.6	67.4	66.0	62.5	46.7	32.0	31.2	46.5
1936	30.6	14.2	36.6	49.0	59.8	63.7	71.3	69.7	57.6	50.3	32.2	33.0	47.3
1937	8.5	24.3	37.6	43.6	55.0	62.2	70.6	66.2	60.4	51.2	39.4	33.4	46.0
1938	30.4	30.9	38.9	47.6	55.0	65.0	73.2	66.6	66.0	50.3	34.4	32.6	49.2
1939 ¹	33.8	26.7	38.9	49.0	57.2	58.2	68.8	68.4	59.4	47.2	38.6	35.0	48.4
1940	27.6	34.8	42.8	49.0	57.5	64.6	70.2	67.8	62.6	52.0	32.4	32.6	49.5
1941	30.8	36.2	44.1	50.1	55.3	60.2	70.5	66.6	54.8	46.9	39.4	32.8	49.0
1942	23.1	30.1	38.4	49.2	52.7	58.2	68.8	69.2	61.0	50.4	35.6	32.5	47.4
1943	24.1	32.4	32.4	48.4	51.2	56.8	67.4	68.0	62.2	51.6	39.8	29.9	47.0
1944	29.4	31.2	35.4	47.4	55.7	61.8	68.5	66.3	61.2	51.1	36.8	28.6	47.8
1945	33.5	34.6	37.4	44.0	56.0	60.4	69.2	68.6	55.9	50.4	37.4	30.5	48.2
1946	31.4	33.6	40.8	47.4	55.2	58.2	68.4	67.8	58.3	43.2E	34.4	32.6	47.6
1947	25.4	34.5	41.5	47.6	58.4	59.5	69.0	66.2	58.0E	49.9	35.4	33.6	48.3
1948	28.6	30.0	35.6	43.8	54.1	64.9	65.1	65.2	57.8	45.9	36.1	24.9	46.0
1949	11.2	26.9	36.6	49.5	58.0	62.0	68.1	68.6	60.3	43.9	41.0	31.0	46.4
1950	13.9	30.2	35.7	44.0	52.8	61.4	69.1	69.9	60.7	46.8	37.4	36.1	46.5

(con.)

Table 8 (Con.)

Coeur d'Alene (Con.)

Year	Mean temperature												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
	°F												
1951	29.6	32.5	33.5	47.3	55.1	59.1	68.8	67.9	59.4	46.7	36.4	25.9	46.8
1952	26.0	31.5	35.9	47.1	56.5	61.2	68.8	69.3	62.8	52.6	35.0	32.2	48.2
1953	39.3	36.1	39.9	45.9	53.6	58.0	68.1	68.7	61.4	51.4	41.0	35.5	49.9
1954	28.8	35.9	36.2	44.2	55.0	57.7	67.1	64.2	58.4	44.2	42.9	31.3	47.2
1955 ²	29.2	29.4	31.1	41.6	51.1	61.9	66.3	68.5	60.7	50.3	32.2	29.6	46.0
1956	30.7	26.1	36.1	50.1	57.9	60.4	70.6	68.2	61.3	48.2	35.4	33.4	48.2
1957 ²	19.0	29.4	36.7	46.5	58.8	61.6	66.9	64.7	62.0	46.2	36.4	36.4	47.1
1958	32.8	39.6	39.4	46.5	62.6	66.3	71.2	73.8	59.9	50.5	37.5	34.3	51.2
1959	30.6	32.1	39.6	47.7	50.5	62.5	71.3	66.4	57.9	47.5	33.3	32.1	47.6
1960	24.1	31.2	37.9	45.7	52.4	62.3	73.7	65.5	60.6	51.3	38.0	29.1	47.7
1961	32.7	37.5	39.4	45.0	55.3	67.5	72.1	74.5	56.9	48.2	34.4	29.6	49.4
1962	23.9	32.3	33.8	48.6	52.3	61.6	67.5	66.8	61.4E	49.4	39.4	35.4	47.8
1963	22.0	36.3	39.2	45.3	55.2	62.8	67.0	69.9	66.2	52.9	40.3	29.5	48.9
1964	32.3	32.9	35.4	43.8	53.6	61.7	69.4	63.4	56.7	49.5	36.6	27.4	46.9
1965	32.4	33.0	33.7	46.8	53.0	60.8	69.5	68.3	54.3	53.1	40.0	33.1	48.2
1966	30.8	32.6	37.7	45.5	54.9	59.2	69.0	68.4	65.1	50.2	38.8	34.9	49.1
1967	34.9	36.8	38.0	43.4	54.3	63.9	70.5	73.6	67.6	50.6	38.4	30.0	50.2
1968	29.5	37.8	42.0	43.1	53.0	61.6	70.6	66.1	60.6	47.5	37.3	27.1	48.0
1969	20.3	29.7	36.1	48.2	58.2	64.3	67.2	68.0	61.8	46.3	40.2	32.3	47.7
1970	28.8	37.4	38.8	42.5	56.2	66.3	72.4	70.5	55.4	47.6	39.0	31.3	48.9
1971	32.7	35.2	36.6	46.2	56.4	59.2	68.5	73.4	56.0	46.7	37.6	29.0	48.1
1972	26.5	33.4	42.4	43.2	56.9	62.1	66.9	71.9	56.3	49.4	39.9	27.6E	48.0
1973	28.0	35.1	40.8	47.0	56.6	63.1	71.0	70.5	61.5	49.8	35.1	35.3	49.5
1974	27.1	36.9	39.4	46.7	50.7	64.8	68.3	68.4	61.7	51.2	40.3	34.5	49.2
1975	29.0	29.9	36.2	42.6	52.8	59.0	72.2E	64.8	60.5	48.9	37.2	33.9	47.3
1976	33.5	34.2	35.7	45.9	56.2	58.8	68.1	66.0	63.1	49.8	39.1	33.2	48.6
1977	27.0	36.8	38.3	51.4	53.2	65.9	67.9	71.1	57.2	48.8	36.4	31.0	48.8
1978	31.6	35.9	42.3	47.5	52.6	63.5	67.7	65.7	58.5	49.6	34.6	26.2	48.0
1979	17.1	32.1	40.9	46.2	55.1	62.3	70.1	71.0	63.3	51.9	34.9	36.2	48.4
1980	25.1	35.6	38.4	51.3	56.7	59.5	67.3	64.6	60.9	50.6	39.5	36.0	48.8
1981	35.2	36.3	43.9	47.4	53.7	57.4	66.1	72.0	61.4	47.2	40.5	32.2	49.4
1982	29.6	31.7	40.4	43.1	53.5	65.2	66.9	69.4	59.8	47.7	35.9	31.8	47.9
1983	36.5	39.1	44.1	46.9	56.6	61.5	64.0	70.7	56.9	50.3	40.3	22.4	49.1
1984	31.6	35.8	41.7	46.0	51.4	59.9	69.6	71.3	57.0	46.2	38.0	27.0	48.0
1985	26.6	28.2	37.8	49.2	57.8	62.7	75.5	65.6	54.4	47.6	27.3	25.5	46.5
10-year averages													
1921-30	25.2	31.2	38.6	46.3	55.0	61.8	69.2	67.1	57.1	47.7	36.1	28.2	46.9
1931-40	28.2	28.1	38.5	47.3	55.8	62.6	69.7	67.9	59.7	49.1	36.4	31.9	47.9
1941-50	25.1	32.0	37.8	47.1	54.9	60.3	68.4	67.6	59.0	48.0	37.3	31.3	47.4
1951-60	29.0	32.4	36.6	46.3	55.4	61.1	69.3	67.7	60.4	48.9	36.8	32.0	48.0
1961-70	28.8	34.6	37.4	45.2	54.6	63.0	69.5	69.0	60.6	49.5	38.4	31.1	48.5
1971-80	27.8	34.5	39.1	46.8	54.7	61.8	68.8	68.7	59.9	49.7	37.5	32.3	48.5
30-year averages													
1921-50	26.2	30.4	38.3	46.9	55.2	61.6	69.1	67.5	58.6	48.3	36.6	30.5	47.4
1951-80	28.5	33.8	37.7	46.1	54.9	62.0	69.2	68.5	60.3	49.4	37.6	31.8	48.3
50-year average													
1931-80	27.8	32.3	37.9	46.5	55.1	61.7	69.2	68.2	59.9	49.2	37.3	31.7	48.1

(con.)

Table 8 (Con.)

Kellogg - Observation time mostly about 0900 P.s.t.; 1600 during 1970-73 and 0800 beginning in 1975

Year	Mean temperature												Annual
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
	°F												
1905	(29.8)	27.4E	41.8	46.4	51.4	57.6	65.6	63.6	56.2	41.4	35.6	28.2	45.4
1906	30.6	34.5	34.9	47.8	53.1	56.1	69.4	63.8	56.8	48.4	34.8	32.4	46.9
1907	20.1	34.4	38.6	43.2	(53.5)	57.6	64.4	59.0	56.0	51.4	39.8	31.0	45.8
1908	29.8	31.2	37.4	46.0	49.4	56.6	66.8	61.9	56.0	45.4	(37.3)	28.2	45.5
1909	23.1	33.4	38.8	41.2	49.6	58.8	61.8	61.0	57.4	46.6	38.0	25.3	44.6
1910	25.0	25.0	43.4	48.3	53.9	57.8	66.1	59.9	56.4	48.4	37.3	32.2	46.1
1911	27.0	27.0	39.8	43.6	49.2	61.2	64.2	61.2	53.6	44.0	32.2	27.7	44.2
1912	26.2	33.0	35.0	45.0	53.2	61.3	62.0	60.5	51.6	43.7	38.2	30.2	45.0
1913	23.9	23.3	32.4	44.0	52.2	60.4	63.4	65.3	55.6	43.4	38.9	28.2	44.2
1914	34.0E	31.0	41.0	46.8	54.8	57.8	68.0	34.0	54.2	48.4	38.2	22.6	46.7
1915	23.6	34.2	42.5	49.8	52.8	57.8	63.8	70.4	53.6	48.7	34.2	28.8	46.7
1916	16.6	32.5	38.3	44.8	47.8	57.4	63.8	64.4	55.5	44.0	30.6	21.4	43.1
1917	24.2	29.4	29.0	41.4	51.4	56.3	67.1	65.7	60.0	45.7	39.5	38.0	45.6
1918	31.2	30.5	40.0	45.2	50.3	63.7	67.6E	62.3	61.0	50.2	36.4	30.2	47.4
1919	29.2	30.9	39.0	48.2	52.8	59.8	67.3E	65.6	56.2	41.4	32.4	20.5	45.3
1920	29.7E	32.4	36.8	43.2	49.9	57.2	69.0	65.4	55.8	45.8	36.7	30.7	46.0
1921	31.0	32.4E	38.7	43.4	54.4	62.1	65.4	65.6	50.8	48.6	36.0	28.0	46.4
1922	20.2	25.3E	34.8	41.8	52.2	65.2	67.2	67.4	59.0	49.4	34.2	22.0	44.9
1923	32.0	26.1	36.2	44.6	52.9	59.8	69.4E	66.4	59.3	48.9	38.0	29.6E	46.9
1924	23.2	38.0	38.6	45.4	59.0	60.4	68.0E	64.2	57.8	47.9	34.8	23.9E	46.8
1925	32.0	38.6	40.4	49.9	58.1	63.2	70.8	65.1E	58.8	44.4	36.8	34.6	49.4
1926	29.7E	37.9	42.8	53.4	54.9	62.6	70.2	65.2	52.6	50.0	40.2	30.7E	49.1
1927	28.8	34.5	40.2	44.7	51.4	62.8	68.3	66.6	56.4	49.8	39.2	21.0	47.0
1928	29.7	31.0	41.6	44.3	59.2	61.0	69.8	64.5	60.0	48.8	37.9	28.7E	48.0
1929	18.0	22.4	39.4	43.2	54.6	59.8	67.0	68.9	54.0	49.1	33.0	34.3E	45.3
1930	16.4	37.2	40.0	52.0	53.2	59.5	68.4	68.8	58.3	45.4	34.7	23.9	46.5
1931	32.0	32.6	39.0	47.4	57.0	62.0	68.8	67.0	56.8	47.2	31.0	26.4	47.3
1932	25.6	26.8	35.5	47.4	53.7	62.8	65.2	66.4	57.1	47.4	40.5	24.5	46.1
1933	29.3	22.9	37.8	45.6	50.6	62.5	67.8	66.4	54.5	49.0	38.2	37.0	46.8
1934	35.0	38.1	45.4	55.6	60.0	62.7	68.0	67.2	54.0	49.6	42.6	33.0	50.9
1935	28.9	32.9	36.2	43.8	53.9	60.2	67.3	64.3	61.3	46.3	31.8	30.1	46.4
1936	30.4	17.8	37.2	48.8	60.0	64.3	69.8	67.0	57.2	50.7	32.6	33.2	47.4
1937	11.3	26.8	39.8	43.6	55.3	61.2	69.2	63.0	60.7	51.6	40.3	33.5	46.4
1938	30.0	34.9	39.2	47.6	53.7	64.4	71.4	65.3	65.6	50.6	33.2	32.3	49.0
1939	34.0	27.8	40.4	49.8	56.4	58.3	68.4	68.1	59.0	46.8	38.8	35.2	48.6
1940	27.0	36.4	43.4	49.0	57.6	64.2	69.6	67.1	63.0	52.1	31.6	32.7	49.5
1941	31.0	37.9	45.2	50.6	54.8	61.2	71.4	66.4	53.6	46.1	38.6	32.4	49.1
1942	24.1	31.2	39.0	49.2	52.2	57.8	69.4	68.2	60.0	49.2	35.6	32.2	47.3
1943	22.7	33.4	33.8	48.3	50.4	56.2	66.8	63.4	60.3	49.6	36.6	28.6	45.8
1944	28.7	32.0	34.8	47.2	55.6	61.1	66.5	64.0	59.9	52.6	36.0	27.1	47.1
1945	32.1	34.6	36.6	42.5	55.0	57.7	68.2	67.4	54.8	49.8	35.6	30.3	47.0
1946	30.4	33.8	41.2	47.0	55.4	59.4	67.6	67.2	57.4	42.6	33.8	32.1	47.3
1947	25.0	35.2	41.8	47.2	58.2	58.4	68.6	64.6	57.8	50.2	35.8	(33.0)	48.0
1948	27.2	29.4	36.0	44.2	54.4	65.1	64.4	64.6	58.5	48.0	35.8	23.0	45.9
1949	11.2	27.7	38.3	49.4	58.2	60.2	66.1	67.5	60.2	43.7	41.5	29.4	46.1
1950	15.5	29.8	35.7	44.5	52.1	60.8	68.6	68.0	60.6	48.2	37.8	36.0	46.5
1951	28.5	32.8	34.5	47.5	54.1	59.1	69.3	67.2	58.6	46.8	36.4	26.2	46.8
1952	25.1	32.2	36.7	49.6	56.4	60.9	67.5	67.8	61.6	52.1	35.2	30.9	48.0
1953	39.4	35.6	40.3	45.0	52.2	57.6	67.4	67.1	60.6	50.4	40.8	34.8	49.3
1954	29.3	36.5	36.4	44.1	54.3	56.8	66.4	63.0	56.9	45.7	42.3	30.8	46.9
1955	29.0	29.7	30.8	41.4	50.3	61.9	65.7	66.1	58.0	48.1	30.1	29.5	45.1
1956	29.9	24.8	35.2	48.6	57.1	59.6	68.9	64.1	58.0	46.7	34.3	32.6	46.7
1957	18.0	29.5	37.4	46.4	59.0	61.9	66.6	64.9	60.8	46.7	35.2	34.6	46.8
1958	31.4	39.8	39.5	45.4	62.6	65.4	70.2	71.3	57.8	48.8	36.9	33.6	50.2
1959	30.5	31.0	38.6	46.8	50.6	62.0	68.0	64.1	55.6	46.7	31.6	31.1	46.4
1960	22.5	30.6	37.6	45.9	52.3	61.0	71.9	63.4	59.1	48.3	37.2	28.8	46.6

(con.)

Table 8 (Con.)

Kellogg (Con.)

	Mean temperature												
Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
	°F												
1961 ³	32.0	38.0	39.6	45.0	53.7	66.8	70.1	72.8	54.4	45.7	32.3	28.4	48.2
1962	24.1	32.8	35.7	48.8	51.9	60.4	65.5	64.1	59.2	49.4	39.9	34.1	47.2
1963	19.3	38.2	40.6	45.2	55.3	61.3	64.9	67.4E	64.5	51.8	39.8	28.6	48.1
1964	30.8	31.6	34.8	43.6	51.6	60.9	68.0	62.1	54.5	48.4	36.6	28.1	45.9
1965 ⁴	32.5	33.4	34.1	47.9	52.4	60.1	68.4	66.5	51.8	50.8	40.4	31.8E	47.5
1966 ⁵	(30.1)	(32.6)	(37.7)	(45.4)	(56.6)	(58.2)	(66.8)	(66.0)	(63.2)	(48.0)	(38.2)	(34.1)	(48.1)
1967	(33.4)	(36.1)	(37.5)	(42.6)	(53.4)	(63.1)	(69.6)	(71.6)	(65.5)	(48.3)	(37.2)	(28.8)	(49.0)
1968	(28.7)	(37.9)	(42.8)	(43.6)	(52.8)	(60.8)	(69.1)	(64.0)	(58.6)	(46.4)	(36.6)	(26.0)	(47.3)
1969	(20.3)	(30.6)	(36.8)	(48.0)	(57.6)	(63.5)	(66.0)	(66.4)	(60.0)	(44.9)	(38.6)	(31.1)	(47.0)
1970 ⁴	(28.4)	(37.5)	(38.0)	(41.4)	(56.0)	66.2	71.1	68.8	55.3	46.6	38.7	31.3	48.3
1971	32.0	33.4	36.1	47.0	58.1	59.3	69.1	73.4	55.2	45.5	36.9	28.0	47.8
1972	26.3	33.1	42.2	42.9	56.6	61.6	66.3	70.2	56.2	47.1	37.7	26.3	47.2
1973 ⁶	28.3	34.9	39.4	44.8	55.8	60.5	67.5	66.2	(59.3)	(47.6)	(34.0)	(34.0)	48.1
1974	(25.3)	(35.8)	(38.7)	(46.1)	(50.4)	(64.8)	(67.7)	(66.6)	(59.9)	(49.6)	(38.5)	(32.7)	(48.0)
1975 ⁴	(28.1)	29.3	36.1	42.5	51.8	58.8	73.0	64.2	60.0	48.0	35.2	31.4	46.5
1976	31.2	33.5	35.4	46.1	56.3	58.6	68.5	65.1	63.1	47.8	37.2	29.7	47.7
1977	25.1	36.6	38.2	50.1	51.5	66.6	66.6	70.4	55.5	46.5	35.1	29.2	47.6
1978	30.2	35.7	43.0	48.0	52.0	63.6	68.1	64.9	57.6	47.6	31.6	22.8	47.1
1979	15.2	30.7	40.4	45.7	55.8	62.6	68.3	69.1	61.5	49.3	32.7	35.0	47.2
1980	23.2	33.8	37.3	50.6	54.0	58.4	68.2	64.0	58.1	49.1	38.8	34.2	47.5
1981	35.4	35.7	43.0	46.6	54.4	57.4	67.1	71.4	59.7	45.3	39.5	30.7	48.9
1982	26.9	30.2	40.6	43.6	53.6	65.9	66.6	68.3	58.6	46.7	33.2	29.8	47.0
1983	34.7	37.8	42.6	46.4	55.9	61.1	63.7	69.7	53.9	45.1	38.6	18.8	47.4
1984	27.9	34.6	40.5	44.8	50.5	58.8	69.1	69.2	53.9	43.3	35.6	23.2	46.0
1985	22.8	25.0	35.6	47.3	56.7	61.5	73.5	64.0	52.9	43.8	24.8	19.9	44.0
10-year averages													
1911-20	26.6	30.4	37.4	45.2	51.4	59.3	65.6	64.5	55.7	45.5	35.7	27.8	45.4
1921-30	26.1	32.3	39.3	46.3	55.0	61.6	68.5	66.3	56.7	48.2	36.5	27.7	47.0
1931-40	28.4	29.7	39.4	47.9	55.8	62.3	68.6	66.2	58.9	49.1	36.1	31.8	47.8
1941-50	24.8	32.5	38.2	47.0	54.6	59.8	67.8	66.1	58.3	48.0	36.7	30.4	47.0
1951-60	28.4	32.3	36.7	46.1	54.9	60.6	68.2	65.9	58.7	48.0	36.0	31.3	47.3
1961-70	28.0	34.9	37.8	45.2	54.1	62.1	68.0	67.0	58.7	48.0	37.8	30.3	47.7
1971-80	26.5	33.7	38.7	46.4	54.2	61.5	68.3	67.4	58.6	47.8	35.8	30.3	47.5
30-year averages													
1921-50	26.4	31.5	39.0	47.1	55.1	61.2	68.3	66.2	58.0	48.4	36.4	30.0	47.3
1951-80	27.6	33.6	37.7	45.9	54.4	61.4	68.2	66.8	58.7	47.9	36.5	30.6	47.4
50-year average													
1931-80	27.2	32.6	38.2	46.5	54.7	61.3	68.2	66.5	58.6	48.2	36.5	30.8	47.4

¹Station relocated during this year; see footnotes in table 5.²Equipment moved short distance; see table 5.³Equipment moved short distance; see footnote in table 5.⁴Station relocated during this year; see table 5.⁵Mean temperatures estimated during 1966-70 because of significantly lower minimum temperatures apparent at airport location. Estimates based on departures from 1941-70 normals at Coeur d'Alene, St. Marys, and Wallace (Woodland Park), ID.⁶No observations during September 1973 to January 1975. Values estimated as described in preceding footnote.

Table 9--Daily maximum and minimum temperature statistics for indicated years of record. Based on 24-hour period ending about 1630 P.s.t. at Deception Creek; mostly 1500 to 1600 at other stations, except morning observation time at Coeur d'Alene prior to year 1941. Letter "M" following year number in table denotes occurrence of missing data; average shown is based on at least 7 days of data during 10-day (or 11-day) period

MAXIMUM DAILY TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION		DECEPTION CREEK HQ						1936-1945									
		10-DAY AND MONTHLY PERIOD MEANS						10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.	MEAN	STD.	MEDIAN	HIGHEST	LOWEST		HIGH.	AVG.	STD.	MEDIAN	LOW.	AVG.	STD.	MEDIAN	PRD.	
BEGINS	YRS		DEV.		AVG.YR	AVG.YR		HIGH.YR	HIGH	DEV.	HIGH	LOW.YR	LOW	DEV.	LOW	BEGINS	
MAY	1	9	62.4	4.8	62.0	68.2 45	I	81 36	73.9	6.3	75.0	45 43	50.1	4.8	49.0	MAY	1
MAY	11	9	63.0	5.9	63.0	71.2 39	I	86 39	74.7	9.2	76.0	47 43	52.7	4.8	53.0	MAY	11
MAY	21	10	69.1	4.5	67.5	77.3 36	I	92 36	80.4	5.6	81.0	42 44	54.4	5.3	55.0	MAY	21
JUN	1	10	67.1	4.0	66.5	74.2 38	I	85 37	76.5	4.7	75.0	46 43	55.4	6.6	55.0	JUN	1
JUN	11	10	69.4	6.9	68.5	84.8 40	I	94 40	78.1	8.3	76.0	54 45	58.9	6.5	55.5	JUN	11
JUN	21	10	76.3	4.4	75.0	82.9 36	I	95 36	87.6	4.4	87.5	57 37	63.8	7.1	61.0	JUN	21
JUL	1	10	80.1	4.0	80.0	85.9 42	I	93 39	88.0	3.8	88.5	64 39	70.7	5.3	72.0	JUL	1
JUL	11	10	82.3	5.3	82.0	89.2 41	I	98 41	91.2	4.3	91.5	61 43	71.5	7.2	70.0	JUL	11
JUL	21	10	83.2	3.9	83.0	88.0 39	I	98 39	91.6	4.3	90.5	60 40	72.7	6.5	74.5	JUL	21
AUG	1	10	80.8	4.2	79.5	86.5 42	I	92 42	89.3	3.0	90.5	59 37	72.4	6.6	72.0	AUG	1
AUG	11	10	80.2	4.6	80.5	86.5 40	I	93 42	86.9	4.3	87.5	60 38	72.2	6.5	74.5	AUG	11
AUG	21	10	76.9	4.9	76.5	83.7 38	I	93 40	87.6	4.2	87.5	54 45	64.3	6.5	65.0	AUG	21
SEP	1	10	73.1	5.6	72.0	81.3 44	I	93 38	83.9	7.1	86.0	51 40	58.7	4.9	58.5	SEP	1
SEP	11	9	69.2	9.2	69.0	83.9 38	I	92 38	81.6	10.1	86.0	44 36	58.1	9.5	57.0	SEP	11
SEP	21	9	69.3	6.1	70.0	77.7 38	I	88 43	77.7	7.7	79.0	51 37	60.2	6.2	61.0	SEP	21
OCT	1	9	60.1	7.2	58.0	73.6 45	I	81 43	68.8	8.0	69.0	43 41	50.9	5.5	50.0	OCT	1
OCT	11	9	56.2	4.4	55.0	61.3 36	I	70 40	63.3	5.5	65.0	41 43	49.2	4.5	50.0	OCT	11
OCT	21	9	50.0	4.2	49.0	57.1 37	I	63 39	58.4	3.5	58.0	35 43	41.9	5.0	42.0	OCT	21
MONTH																	MONTH
MAY	9	64.9	3.8	64.0	70.2 40	58.3 43	I	92 36	82.1	5.6	83.0	42 44	47.8	3.9	47.0	MAY	
JUN	10	70.9	4.0	71.0	77.8 40	65.4 43	I	95 36	88.3	4.8	88.5	46 43	53.5	4.8	54.0	JUN	
JUL	10	81.9	1.3	81.5	84.0 41	80.2 43	I	98 41	94.2	3.0	94.0	60 40	64.9	3.4	64.5	JUL	
AUG	10	79.2	3.0	79.0	83.1 40	74.1 37	I	93 42	90.8	2.5	92.0	54 45	62.1	5.8	61.5	AUG	
SEP	9	70.6	5.3	71.0	78.1 38	59.0 41	I	93 38	84.9	6.7	87.0	44 36	53.1	5.3	52.0	SEP	
OCT	9	55.3	2.3	55.0	59.4 36	51.5 41	I	81 43	70.9	5.5	70.0	35 43	41.7	4.8	42.0	OCT	

MINIMUM DAILY TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION		DECEPTION CREEK HQ						1936-1945									
		10-DAY AND MONTHLY PERIOD MEANS						10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.	MEAN	STD.	MEDIAN	HIGHEST	LOWEST		HIGH.	AVG.	STD.	MEDIAN	LOW.	AVG.	STD.	MEDIAN	PRD.	
BEGINS	YRS		DEV.		AVG.YR	AVG.YR		HIGH.YR	HIGH	DEV.	HIGH	LOW.YR	LOW	DEV.	LOW	BEGINS	
MAY	1	9	31.5	3.3	31.0	35.9 41	I	50 41	38.2	5.7	39.0	22 39	26.1	3.2	27.0	MAY	1
MAY	11	9	34.7	3.5	35.0	39.2 41	I	53 41	42.9	6.1	42.0	24 42	27.8	3.5	27.0	MAY	11
MAY	21	10	38.3	2.7	38.0	42.8 42	I	53 42	48.9	2.8	49.0	27 40	30.2	3.0	30.0	MAY	21
JUN	1	10	39.3	3.3	39.5	43.8 36	I	54 44	46.1	3.5	46.0	25 39	32.3	4.4	33.5	JUN	1
JUN	11	10	41.7	2.5	41.5	45.1 41	I	52 37	48.8	2.4	49.0	30 45	33.7	3.4	33.5	JUN	11
JUN	21	10	42.9	2.9	43.0	46.5 38	M I	58 37	50.2	4.2	49.0	29 39	34.8	3.8	34.5	JUN	21
JUL	1	10	43.3	2.5	42.0	46.9 36	I	56 41	50.5	3.1	50.5	32 44	36.5	2.8	35.5	JUL	1
JUL	11	10	44.2	3.1	43.5	48.8 41	I	56 41	51.6	3.0	51.5	30 43	36.0	3.8	35.5	JUL	11
JUL	21	10	44.3	1.8	44.5	46.8 40	I	59 44	52.7	5.0	53.0	32 45	36.6	3.0	37.0	JUL	21
AUG	1	10	40.9	3.0	40.5	44.2 42	I	56 45	49.2	5.0	50.0	29 38	34.7	3.1	34.5	AUG	1
AUG	11	10	40.5	2.7	40.5	45.6 41	I	55 41	48.8	5.2	49.0	29 45	32.0	2.5	32.0	AUG	11
AUG	21	10	39.4	2.7	39.5	44.7 41	I	51 41	46.7	2.7	46.0	28 37	32.2	2.3	32.0	AUG	21
SEP	1	10	40.6	3.3	40.5	44.1 41	I	53 36	48.9	3.5	49.5	28 43	32.9	3.2	33.0	SEP	1
SEP	11	9	38.1	4.6	38.0	47.1 40	I	52 40	45.1	4.9	45.0	24 43	31.7	5.3	32.0	SEP	11
SEP	21	9	35.7	4.7	33.0	44.9 40	I	52 40	43.8	5.2	42.0	23 37	28.8	5.3	28.0	SEP	21
OCT	1	9	36.1	3.3	36.0	40.4 38	I	47 43	43.2	3.5	44.0	25 36	29.9	3.2	30.0	OCT	1
OCT	11	9	34.2	3.8	33.0	42.1 40	I	51 40	42.8	3.7	42.0	20 38	27.6	5.4	27.0	OCT	11
OCT	21	9	32.0	4.6	32.0	39.5 37	I	46 40	40.0	4.6	41.0	18 42	25.0	5.8	26.0	OCT	21
MONTH																	MONTH
MAY	9	35.0	2.7	36.0	38.5 41	30.4 37	I	53 42	49.4	3.2	51.0	22 39	25.3	2.7	24.0	MAY	
JUN	10	41.3	2.1	40.0	44.5 36	38.1 39	M I	58 37	51.0	3.4	49.5	25 39	30.5	3.0	30.5	JUN	
JUL	10	43.9	1.5	43.0	46.9 41	42.3 43	I	59 44	54.6	3.1	54.0	30 43	33.7	2.6	33.5	JUL	
AUG	10	40.2	2.4	39.0	44.8 41	36.2 38	I	56 45	51.3	3.3	51.5	28 37	31.1	2.1	31.5	AUG	
SEP	9	38.0	3.5	36.0	45.2 40	33.4 43	I	53 36	49.7	2.6	50.0	23 37	27.7	4.8	26.0	SEP	
OCT	9	34.0	2.9	33.0	39.5 40	29.1 36	I	51 40	44.9	3.0	44.0	18 42	23.1	4.8	22.0	OCT	

(con.)

Table 9 (Con.)

MAXIMUM DAILY TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 101956										COVER D'ALENE										1931-1980							
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES																	
PRD.	NO.	MEAN	STD.	MEDIAN	HIGHEST	LOWEST				HIGH	AVG.	STD.	MEDIAN	LOW	AVG.	STD.	MEDIAN	PRD.									
BEGINS	YRS		DEV.		AVG.YR	AVG.YR				YR	HIGH	DEV.	HIGH	YR	LOW	DEV.	LOW	BEGINS									
JAN	1	49	34.1	6.1	34.0	43.4 53	19.7 74	I		56 53	41.9	6.2	42.0	10 49	26.3	7.6	29.0	JAN									
JAN	11	49	34.7	6.6	37.0	45.8 53 M	16.6 50	I		52 45	42.7	6.3	44.0	4 50	25.9	9.5	30.0	JAN									
JAN	21	49	34.4	6.9	35.0	45.5 53	15.8 37	I		58 71	43.2	6.9	45.0	3 35	24.8	9.2	27.0	JAN									
FEB	1	50	38.2	6.0	39.0	46.2 34	18.8 36	I		58 62	45.7	5.5	45.0	-2 36	28.9	10.0	32.5	FEB									
FEB	11	50	40.6	6.0	40.5	54.2 77	15.1 36	I		59 77	47.9	6.2	48.0	8 36	33.3	8.2	35.0	FEB									
FEB	21	50	43.3	4.7	43.0	55.3 68	30.9 62	I		62 68	49.6	5.4	49.0	22 57	36.4	5.6	37.0	FEB									
MAR	1	50	44.3	5.2	43.0	56.7 68	35.1 51	I		69 53	52.2	6.5	52.0	23 60	36.5	5.7	37.0	MAR									
MAR	11	50	48.0	4.9	47.0	62.3 34	40.0 43	I		70 72	56.8	6.3	56.0	28 65	40.1	4.9	40.0	MAR									
MAR	21	50	51.1	5.5	51.0	63.2 41	40.4 65	I		73 78	60.9	6.6	61.0	31 64	42.2	5.3	43.0	MAR									
APR	1	50	55.5	5.9	55.0	66.7 42	43.0 35	I		82 77	64.7	6.8	64.0	25 36	46.6	6.0	47.0	APR									
APR	11	50	59.2	6.6	57.0	73.0 43	47.4 55	I		84 43	70.1	7.7	70.0	37 68	48.6	5.9	47.0	APR									
APR	21	48	62.0	6.1	60.5	78.9 77	52.7 70	I		94 77	73.6	8.1	73.0	38 62	51.0	6.3	49.0	APR									
MAY	1	49	65.9	6.2	65.0	80.8 66	50.3 33	I		90 66	76.6	7.6	77.0	45 75	54.5	6.2	54.0	MAY									
MAY	11	49	68.9	5.4	69.0	80.9 73	53.8 74	I		92 39	80.1	6.7	80.0	44 67	57.1	5.8	57.0	MAY									
MAY	21	49	71.6	5.6	71.0	86.6 58	59.9 32	I		95 36	82.6	6.5	84.0	50 60	59.0	5.6	58.0	MAY									
JUN	1	50	73.8	5.4	72.5	85.3 70	65.3 39 M	I		95 70	84.2	5.4	84.5	49 66	62.2	6.6	61.0	JUN									
JUN	11	50	75.4	5.5	74.0	90.9 74	66.3 43	I		98 61	85.6	6.0	84.0	53 38	64.2	6.7	64.0	JUN									
JUN	21	50	77.5	5.1	76.5	84.4 73	65.8 69	I		102 73	88.2	5.8	88.5	54 41	65.3	6.6	64.5	JUN									
JUL	1	50	82.6	5.0	82.0	95.2 75	71.5 35	I		103 75	91.6	6.5	92.0	58 66	71.5	6.8	71.0	JUL									
JUL	11	50	86.3	5.1	86.0	97.1 60	74.3 80	I		105 75	95.7	5.4	97.0	64 78	75.3	6.1	74.0	JUL									
JUL	21	50	88.8	3.9	89.0	96.4 39	79.2 40	I		108 39	97.5	4.4	97.0	59 48	77.9	7.6	79.5	JUL									
AUG	1	50	87.4	5.1	87.0	96.4 71	76.8 57	I		109 61	95.5	4.8	96.0	62 37	77.3	7.2	78.0	AUG									
AUG	11	50	86.7	6.1	86.5	100.0 67	70.1 78	I		103 67	94.7	4.6	95.0	59 78	76.5	8.7	77.5	AUG									
AUG	21	50	82.0	6.0	82.0	92.5 67	67.3 60	I		104 46	92.8	6.1	93.5	56 68	70.3	7.2	71.0	AUG									
SEP	1	50	79.5	5.7	78.0	91.9 55	65.9 47	I		102 67	89.4	6.2	90.0	54 71	67.6	7.9	66.5	SEP									
SEP	11	50	74.6	6.6	74.0	88.5 38	58.8 41	I		98 38	85.7	7.1	86.5	45 47	63.1	7.3	62.0	SEP									
SEP	21	50	71.7	7.9	70.0	86.8 67	57.1 34	I		94 43	80.9	7.7	82.0	41 34	61.1	8.5	60.5	SEP									
OCT	1	50	66.8	6.9	65.5	85.3 43 M	58.2 46	I		87 43	76.2	7.0	78.0	37 46	57.0	8.1	56.0	OCT									
OCT	11	50	61.5	5.0	62.0	72.2 74	47.5 46	I		85 34	70.0	5.9	70.0	36 46	53.4	6.1	53.0	OCT									
OCT	21	50	54.9	5.0	54.0	67.3 65	46.0 71	I		73 69	63.7	5.7	64.0	20 35	46.2	7.0	46.0	OCT									
NOV	1	50	48.5	4.5	48.5	57.0 80 M	37.0 35	I		71 75	55.9	5.3	55.5	27 35	41.0	5.3	41.0	NOV									
NOV	11	49	43.6	4.5	43.0	51.1 76	27.6 55 M	I		61 36	51.1	4.6	51.0	11 55	36.1	6.2	37.0	NOV									
NOV	21	50	41.2	4.0	40.5	50.8 33	30.5 31	I		59 54	48.9	5.4	50.0	23 77	33.9	4.6	34.0	NOV									
DEC	1	50	38.9	4.5	39.0	47.7 39	23.8 72 M	I		57 58	47.7	5.5	48.0	10 32	30.5	5.9	31.0	DEC									
DEC	11	50	36.7	5.4	36.0	45.1 76	24.9 32	I		52 76	44.4	5.2	45.5	4 64	28.9	7.3	31.0	DEC									
DEC	21	50	36.4	4.8	36.0	48.0 80	23.5 68	I		60 33	45.0	5.3	45.0	-4 68	27.6	7.2	29.0	DEC									
MONTH										MONTH										MONTH							
JAN	49	34.4	5.1	35.0	44.9 53 M	19.6 37	I		58 71	47.4	4.3	47.0	3 35	20.0	8.6	20.0	JAN										
FEB	50	40.5	4.5	40.5	48.6 68	23.5 36	I		62 68	52.3	4.5	52.0	-2 36	26.8	9.5	29.5	FEB										
MAR	50	47.9	3.7	47.0	59.1 41	41.0 55	I		73 78	62.2	5.7	62.0	23 60	34.8	5.2	35.0	MAR										
APR	48	58.7	4.2	57.5	68.6 34	52.0 55	I		94 77	75.8	7.1	75.5	25 36	43.9	4.8	44.0	APR										
MAY	49	68.9	3.9	69.0	79.1 58	59.9 33	I		95 36	85.7	4.7	85.0	44 67	51.5	4.2	51.0	MAY										
JUN	50	75.6	3.2	75.0	84.2 61	69.7 53	I		102 73	91.0	4.3	91.0	49 66	58.4	3.8	58.0	JUN										
JUL	50	86.0	2.7	86.0	92.0 60	80.6 48	I		108 39	99.3	4.0	99.0	58 66	68.4	5.3	68.0	JUL										
AUG	50	85.3	4.2	86.0	94.0 67	76.7 64	I		109 61	97.8	4.0	98.0	56 64	68.0	6.4	67.5	AUG										
SEP	50	75.3	5.0	75.0	85.9 67	64.8 41	I		102 67	90.6	5.3	91.0	41 34	57.1	6.1	57.0	SEP										
OCT	50	60.9	4.0	60.0	69.5 52	47.6 46	I		87 43	77.2	5.8	78.0	20 35	45.3	6.3	46.0	OCT										
NOV	49	44.4	2.9	44.0	50.1 54	38.7 35	I		71 75	56.9	4.7	57.0	11 55	32.0	5.4	32.0	NOV										
DEC	50	37.3	2.9	37.0	42.9 57 M	30.4 48	I		60 33	50.2	4.0	50.5	-4 68	23.3	7.4	25.0	DEC										

(con.)

Table 9 (Con.)

MINIMUM DAILY TEMPERATURE										MEAN, STANDARD DEVIATION, AND EXTREME VALUES									
STATION NUMBER 101956 COVER D'ALENE 10-DAY AND MONTHLY PERIOD MEANS							1931-1980 10-DAY AND MONTHLY EXTREME DAILY VALUES												
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG,YR	LOWEST AVG,YR	I	HIGH,YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW,YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS			
JAN 1	49	21.7	9.1	24.0	33.0 54	-1.5 37	I	42 63	31.4	5.7	33.0	-16 37	10.7	11.8	13.0	JAN 1			
JAN 11	49	21.9	9.4	25.0	36.0 53 M	-4.0 49	I	46 53	31.9	6.9	33.0	-27 35	8.9	14.2	12.0	JAN 11			
JAN 21	49	19.8	9.5	21.0	35.0 53 M	-3.9 57	I	48 71	31.8	6.8	33.0	-30 50	5.1	14.4	7.0	JAN 21			
FEB 1	50	22.4	8.3	25.0	32.3 61	-2.2 33	I	44 45	32.4	5.6	33.0	-29 33	9.2	15.6	15.5	FEB 1			
FEB 11	50	24.1	7.6	25.0	33.6 58	-9.0 36	I	42 58	32.9	5.3	33.0	-21 36	14.0	11.3	16.0	FEB 11			
FEB 21	50	25.7	5.5	27.0	33.5 58	10.4 62	I	44 61	33.4	3.7	34.0	-5 57	17.7	8.5	20.0	FEB 21			
MAR 1	50	25.3	4.6	25.0	32.7 34	10.4 43	I	41 72	33.9	3.7	33.5	-13 55	14.7	9.0	16.5	MAR 1			
MAR 11	50	28.0	3.9	28.0	37.0 72	19.0 43	I	43 40	35.2	3.2	35.0	-1 56	19.5	7.7	21.0	MAR 11			
MAR 21	50	29.9	3.4	30.0	38.0 78	21.5 65	I	46 70	37.4	3.3	37.0	7 55	22.0	5.6	23.5	MAR 21			
APR 1	50	31.8	2.8	31.5	38.7 34	24.5 35	I	48 61	39.8	3.6	40.0	5 36	24.2	4.6	25.0	APR 1			
APR 11	50	33.8	2.3	33.0	40.8 36	29.1 70	I	48 38	41.5	2.9	41.5	19 66	26.8	3.3	27.0	APR 11			
APR 21	49	36.3	3.2	36.0	45.1 34	30.5 50	I	51 80	44.0	3.8	44.0	18 51	29.1	4.0	29.0	APR 21			
MAY 1	49	38.8	3.1	38.0	46.6 80	32.6 35	I	53 47	46.6	3.3	47.0	21 54	31.1	4.3	30.0	MAY 1			
MAY 11	49	40.9	2.9	40.0	47.3 57	31.8 43	I	57 31	49.2	4.4	49.0	27 55	32.8	3.4	32.0	MAY 11			
MAY 21	49	43.5	3.1	43.0	52.6 58	38.4 50	I	60 61	52.6	4.0	53.0	21 51	35.5	4.3	35.0	MAY 21			
JUN 1	50	46.4	3.2	46.0	53.1 69	40.1 51	I	65 58	54.5	4.5	54.0	29 51	38.8	3.6	39.0	JUN 1			
JUN 11	50	47.8	3.0	47.5	54.1 63	40.8 46	I	65 63	55.6	3.7	55.0	28 46	40.2	4.1	40.0	JUN 11			
JUN 21	50	49.3	3.2	48.0	57.1 38	42.9 43	I	65 37	56.9	3.7	56.0	34 46	42.1	4.0	43.0	JUN 21			
JUL 1	50	50.7	3.0	50.0	57.1 70	44.1 44	I	66 31	58.4	3.3	59.0	36 71	43.1	3.9	43.0	JUL 1			
JUL 11	50	52.7	2.7	52.0	59.8 38	45.8 43	I	70 67	60.6	3.9	61.0	37 45	45.5	3.8	45.0	JUL 11			
JUL 21	50	53.4	2.7	53.0	59.2 38	46.8 54	I	69 37	61.3	4.0	61.0	36 51	45.7	3.9	46.0	JUL 21			
AUG 1	50	52.3	3.0	51.0	58.9 71	44.6 46	I	71 61	60.2	3.9	61.0	38 47	45.3	4.5	45.5	AUG 1			
AUG 11	50	51.5	2.8	51.0	58.0 34 M	45.6 40	I	69 61	59.5	4.0	59.0	33 45	43.8	4.6	44.0	AUG 11			
AUG 21	50	49.7	2.2	49.0	56.0 61	45.4 47	I	66 67	57.3	3.0	57.0	35 45	41.7	3.2	42.0	AUG 21			
SEP 1	50	47.2	3.1	47.0	54.4 67	40.2 48	I	62 67	55.5	3.4	56.0	31 62	39.2	3.9	39.0	SEP 1			
SEP 11	50	44.5	3.4	44.0	51.7 80	37.5 70	I	59 68	53.1	3.7	54.0	24 34	36.5	5.2	37.0	SEP 11			
SEP 21	50	41.7	3.7	40.5	49.0 38	34.1 34	I	60 67	50.7	4.3	51.0	24 34	33.8	4.8	34.0	SEP 21			
OCT 1	48	39.4	2.7	39.0	45.9 51 M	35.0 74	I	55 65	48.1	3.2	48.0	22 50	31.9	3.7	31.5	OCT 1			
OCT 11	49	37.5	3.6	37.0	44.4 40	28.4 49	I	57 40	46.3	3.8	47.0	19 49	30.0	4.2	30.0	OCT 11			
OCT 21	50	35.4	3.3	35.0	43.4 37	25.5 35	I	53 37	44.2	3.8	45.0	2 35	26.9	5.4	27.0	OCT 21			
NOV 1	50	32.0	4.6	31.5	42.6 80 M	17.6 35	I	49 78	40.3	4.5	40.0	0 35	23.8	6.7	25.0	NOV 1			
NOV 11	49	30.0	5.5	30.0	38.4 54	8.6 55 M	I	47 32	38.3	3.7	39.0	-12 55	21.9	8.8	24.0	NOV 11			
NOV 21	50	28.4	4.9	29.0	37.3 49 M	7.3 31	I	46 49	36.5	5.3	37.0	0 31	20.3	6.5	21.0	NOV 21			
DEC 1	50	27.5	4.5	28.0	33.8 79	8.3 72 M	I	47 75	36.2	4.0	36.0	-7 72	17.4	8.2	19.0	DEC 1			
DEC 11	50	25.6	6.8	26.0	35.2 62	9.0 64	I	41 62	34.0	4.4	34.0	-16 64	16.3	10.5	19.5	DEC 11			
DEC 21	50	25.2	5.7	25.5	36.9 80	9.5 68	I	48 80	34.8	4.5	34.5	-26 68	13.1	10.1	14.5	DEC 21			
MONTH							I										MONTH		
JAN	49	21.1	7.3	22.0	33.7 53 M	-2.3 37	I	48 71	35.7	4.5	35.0	-30 50	-0.2	12.7	1.0	JAN			
FEB	50	24.0	5.2	24.0	32.5 58	4.1 36	I	44 61	36.1	2.9	36.0	-29 33	4.9	13.6	10.0	FEB			
MAR	50	27.8	2.8	27.5	32.5 72	20.9 43	I	46 70	38.2	2.9	38.5	-13 55	12.7	8.7	14.5	MAR			
APR	49	34.0	1.9	33.0	39.8 34	29.9 51	I	51 80	45.2	3.0	45.0	5 36	23.2	4.3	24.0	APR			
MAY	49	41.2	2.1	41.0	46.1 58	37.5 43	I	60 61	53.5	3.5	54.0	21 54	29.6	3.3	30.0	MAY			
JUN	50	47.8	2.4	47.0	51.8 36	42.1 46	I	65 63	58.9	3.3	59.0	28 46	37.6	3.5	38.0	JUN			
JUL	50	52.3	2.1	52.0	57.9 38	48.6 51	I	70 67	63.2	3.0	63.0	36 71	41.8	3.1	42.0	JUL			
AUG	50	51.1	2.1	51.0	55.6 61	47.6 40	I	71 61	62.1	3.3	62.0	33 45	40.8	3.3	40.0	AUG			
SEP	50	44.5	2.4	44.0	49.5 63	40.4 43	I	62 67	56.9	2.4	57.0	24 34	32.2	4.1	31.0	SEP			
OCT	48	37.4	2.1	37.0	42.2 40	32.7 49	I	57 40	49.5	3.0	49.0	2 35	25.9	5.1	26.0	OCT			
NOV	49	30.1	3.3	30.0	36.3 34	21.0 36	I	49 78	42.2	3.5	42.0	-12 55	16.2	8.4	18.0	NOV			
DEC	50	26.1	3.4	26.0	31.4 50	17.8 32	I	48 80	38.5	3.7	38.0	-26 68	8.0	10.2	11.0	DEC			

(con.)

Table 9 (Con.)

MAXIMUM DAILY TEMPERATURE

STATION NUMBER 100304 FERNAN RS										1951-1970									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.																		
BEGINS	YRS	MEAN	STD.	MEDIAN	HIGHEST	LOWEST													PRD.
			DEV.		AVG. YR	AVG. YR			HIGH, YR	AVG.	STD.	MEDIAN		AVG.	STD.	MEDIAN			BEGINS
										HIGH	DEV.	HIGH		LOW, YR	LOW	LOW			
MAY	1	14	65.5	6.7	63.5	80.8 66			90 66	76.6	8.0	77.0		46 64	53.9	5.6	53.0		MAY 1
MAY	11	16	69.6	4.3	69.5	75.8 54			90 56	80.6	5.5	80.5		44 67	56.4	6.7	58.0		MAY 11
MAY	21	17	72.0	6.5	70.0	86.7 58			93 58	81.6	6.9	84.0		50 60	60.1	7.8	58.0		MAY 21
JUN	1	19	74.5	5.7	73.0	85.3 70			95 70	84.3	5.8	83.0		49 66	63.1	7.1	62.0		JUN 1
JUN	11	19	75.7	5.0	75.0	84.6 63			92 70	85.7	5.3	86.0		55 56	64.4	6.1	64.0		JUN 11
JUN	21	20	77.0	4.8	76.0	84.6 70			98 58	86.4	5.6	85.5		55 69	64.9	4.1	65.0		JUN 21
JUL	1	20	83.1	5.0	83.0	94.0 68			99 68	92.3	3.9	92.5		58 66	71.4	6.7	72.5		JUL 1
JUL	11	20	87.9	4.8	87.5	97.1 60			103 60	95.9	4.2	97.0		65 63	78.0	6.0	78.5		JUL 11
JUL	21	20	88.8	4.3	89.0	94.7 62			106 59	96.0	4.1	96.0		67 65	78.8	7.1	80.0		JUL 21
AUG	1	20	87.6	5.4	88.0	96.3 61			109 61	95.3	6.0	96.0		64 62	77.8	6.5	80.0		AUG 1
AUG	11	20	87.3	6.1	87.0	100.2 67			103 67	94.6	4.8	94.5		60 59	77.1	9.6	77.5		AUG 11
AUG	21	20	80.9	7.2	80.5	92.5 67			103 67	92.1	7.7	91.0		56 64	69.3	8.5	68.0		AUG 21
SEP	1	20	80.5	6.4	80.0	91.9 55			102 67	88.9	6.5	89.5		57 64	69.9	8.3	70.0		SEP 1
SEP	11	20	75.6	6.2	75.5	83.7 56			96 58	86.6	6.2	87.5		53 65	64.6	6.6	63.5		SEP 11
SEP	21	20	71.9	7.6	69.0	86.8 67			93 67	80.3	8.1	79.0		48 68	61.0	8.1	59.5		SEP 21
OCT	1	18	66.7	5.6	65.0	77.7 52			84 70	77.6	5.2	78.0		44 57	55.4	7.7	54.5		OCT 1
OCT	11	16	60.7	5.4	61.0	71.4 63			79 61	68.5	6.0	68.0		45 51	52.9	4.5	52.5		OCT 11
OCT	21	13	56.6	6.0	57.0	67.4 65			73 69	65.9	6.1	67.0		34 57	47.4	7.4	47.0		OCT 21
MONTH										MONTH									
MAY	16	69.0	3.7	68.0	74.6 52 M	62.9 62			93 58	84.4	4.6	84.5		44 67	51.1	4.5	51.0		MAY
JUN	19	75.6	2.8	75.0	80.8 70	70.1 53			98 58	89.4	4.2	89.0		49 66	58.6	3.6	59.0		JUN
JUL	20	86.7	3.0	87.0	92.7 60	81.4 55			106 59	98.1	3.5	98.5		58 66	69.6	6.2	68.0		JUL
AUG	20	85.1	5.0	86.0	94.1 67	76.9 64			109 61	98.1	4.5	98.0		56 64	67.9	7.6	67.5		AUG
SEP	20	76.0	5.0	76.0	86.1 67	67.7 65			102 67	90.3	5.6	90.5		48 68	58.1	5.2	57.5		SEP
OCT	13	61.2	4.4	60.0	69.5 52	54.5 51 M			84 70	77.7	3.7	78.0		34 57	46.2	5.7	47.0		OCT

MINIMUM DAILY TEMPERATURE

STATION NUMBER 100304 FERNAN RS										1951-1970									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.																		
BEGINS	YRS	MEAN	STD.	MEDIAN	HIGHEST	LOWEST				AVG.	STD.	MEDIAN		AVG.	STD.	MEDIAN			PRD.
			DEV.		AVG. YR	AVG. YR			HIGH. YR	HIGH	DEV.	HIGH		LOW. YR	LOW	DEV.	LOW		BEGINS
MAY	1	14	38.6	2.9	38.5	45.3 57			51 54	46.6	3.0	47.5		21 54	31.0	5.0	30.0		MAY 1
MAY	11	16	41.3	2.5	40.0	47.3 57			55 54	49.6	3.9	48.5		27 55	32.8	4.1	32.0		MAY 11
MAY	21	17	43.9	3.6	43.0	52.6 58			60 58	52.4	4.1	52.0		29 53	36.6	4.8	36.0		MAY 21
JUN	1	19	46.9	3.8	47.0	53.1 69			65 58	54.7	4.5	54.0		29 51	39.8	3.8	40.0		JUN 1
JUN	11	19	47.7	2.6	47.0	54.1 63			65 63	55.9	4.1	55.0		34 52	40.0	3.0	40.0		JUN 11
JUN	21	20	48.7	3.0	48.0	55.4 70			64 59	56.6	3.7	56.0		33 51	42.1	3.2	43.0		JUN 21
JUL	1	20	50.2	2.9	50.0	57.1 70			64 70	58.2	3.7	59.0		36 51	42.9	3.5	43.0		JUL 1
JUL	11	20	53.1	2.6	52.0	57.6 70			65 68	60.3	3.8	61.0		40 51	46.5	3.6	46.0		JUL 11
JUL	21	20	53.0	3.1	53.0	57.7 64			68 59	60.8	4.3	61.5		36 51	45.5	3.8	45.5		JUL 21
AUG	1	20	52.5	3.1	53.0	57.4 65			71 61	59.8	4.2	61.0		38 51	46.2	3.8	46.0		AUG 1
AUG	11	20	51.9	2.3	51.0	56.0 58			69 61	60.4	4.2	59.5		40 51	45.3	2.9	45.0		AUG 11
AUG	21	20	50.1	2.5	48.5	56.0 61			66 67	57.6	3.7	57.0		36 52	42.1	3.3	42.0		AUG 21
SEP	1	20	47.0	3.3	46.5	54.4 67			62 67	55.0	3.7	54.0		30 53	38.9	4.9	38.5		SEP 1
SEP	11	20	45.0	3.1	46.0	49.7 59			59 68	53.8	3.1	54.0		27 65	37.2	5.2	39.5		SEP 11
SEP	21	20	42.7	3.6	42.0	48.5 66			61 66	51.2	4.6	51.5		28 54	34.6	4.3	34.5		SEP 21
OCT	1	18	39.9	2.7	38.5	45.9 51 M			55 65	49.0	3.8	48.5		28 68	32.7	3.5	32.0		OCT 1
OCT	11	16	37.8	3.6	37.5	43.8 55			50 55	45.8	2.9	46.5		25 70	30.8	4.1	30.0		OCT 11
OCT	21	13	35.9	2.5	36.0	40.8 62			50 63	44.2	4.0	45.0		21 51	27.8	3.9	27.0		OCT 21
MONTH										MONTH									
MAY	16	41.3	1.9	40.5	45.7 57	38.6 55	M I		60 58	53.0	2.9	54.0		21 54	29.3	3.5	30.0		MAY
JUN	19	47.7	2.4	47.0	51.8 58	43.0 51	I		65 63	59.2	3.5	59.0		29 51	38.4	3.3	39.0		JUN
JUL	20	52.1	2.2	52.0	56.6 70	47.9 51	I		68 59	62.6	2.8	63.0		36 51	42.1	2.5	42.0		JUL
AUG	20	51.5	2.1	51.0	55.6 61	47.4 51	I		71 61	62.3	3.7	62.0		36 52	42.0	3.1	42.0		AUG
SEP	20	44.9	2.4	44.0	49.1 67	41.0 65	I		62 67	56.8	2.9	56.5		27 65	32.8	4.1	31.5		SEP
OCT	13	38.0	1.8	37.0	41.2 63	35.2 69	I		55 65	50.5	3.3	50.0		21 51	27.2	3.3	27.0		OCT

(con.)

Table 9 (Con.)

MAXIMUM DAILY TEMPERATURE

STATION NUMBER 100409 KINGSTON RS										1951-1970									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR		HIGH,YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW,YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS			
MAY 1	9	63.5	7.8	62.0	80.1 66	53.9 64	I	90 66	74.8	8.4	72.0	43 64	52.0	7.4	52.0	MAY 1			
MAY 11	9	69.0	3.8	69.0	73.4 69 M	61.6 66	I	85 70	78.9	3.9	79.0	43 67	57.4	6.7	60.0	MAY 11			
MAY 21	11	71.4	4.2	71.0	78.2 63	63.3 68 M	I	87 61	81.7	4.2	83.0	54 66	59.6	5.4	58.0	MAY 21			
JUN 1	20	74.2	5.2	73.5	83.8 70	66.8 51	I	94 70	83.6	5.3	83.5	49 66	62.6	6.3	62.0	JUN 1			
JUN 11	20	75.3	5.5	74.5	87.0 61	67.3 54	I	97 61	85.2	5.3	85.5	52 56	63.5	6.7	63.5	JUN 11			
JUN 21	20	75.8	4.9	74.5	84.0 70	64.7 69	I	97 55	85.4	5.8	85.5	54 69	63.6	4.4	63.0	JUN 21			
JUL 1	20	81.4	5.1	82.0	91.7 68	69.9 55	I	97 64	90.6	4.0	90.5	55 66	70.1	6.4	70.5	JUL 1			
JUL 11	20	85.8	4.6	86.0	94.7 60	78.5 63	I	102 67	93.8	4.6	94.5	62 63	75.8	6.3	76.0	JUL 11			
JUL 21	20	86.5	4.1	86.0	92.9 62	80.0 70	I	101 59	93.0	4.0	94.0	65 64	76.5	7.0	78.5	JUL 21			
AUG 1	20	85.8	5.0	86.5	95.9 61	77.0 64	I	107 61	93.1	5.9	94.0	62 62	76.3	6.6	77.0	AUG 1			
AUG 11	20	85.4	5.9	85.0	97.4 67	71.4 68	I	101 61	92.7	4.7	92.0	59 68	75.1	9.3	76.0	AUG 11			
AUG 21	20	79.4	6.9	78.5	90.0 67	66.5 60	I	100 66	90.3	7.2	89.5	57 60	68.1	8.3	67.0	AUG 21			
SEP 1	20	78.9	6.1	78.0	89.3 55	67.8 64	I	98 67	87.2	5.6	87.0	56 64	67.5	7.4	66.5	SEP 1			
SEP 11	20	74.2	6.3	74.5	85.6 53 M	60.2 65	I	95 53	85.8	5.8	86.0	49 65	62.2	6.9	60.0	SEP 11			
SEP 21	20	71.6	8.0	69.0	85.0 63	59.2 59	I	92 67	80.3	8.8	78.0	47 56	59.5	9.1	57.0	SEP 21			
OCT 1	9	67.1	6.6	65.0	78.3 52	55.5 69	I	87 57	77.9	6.3	78.0	46 70	56.7	8.8	54.0	OCT 1			
OCT 11	7	61.3	6.1	61.0	72.7 63 M	54.1 69	I	76 63	70.1	5.8	70.0	47 69	52.9	5.3	52.0	OCT 11			
OCT 21	6	57.7	5.5	56.0	66.1 65 M	50.7 70	I	70 69	67.0	4.2	68.5	44 70	47.8	4.6	46.5	OCT 21			
MONTH							I									MONTH			
MAY	8	68.3	2.7	67.5	72.1 66	65.0 64	I	90 66	84.5	2.8	83.5	43 67	48.4	4.6	50.0	MAY			
JUN	20	75.1	3.1	74.0	83.6 61	70.2 53	I	97 61	88.9	4.1	88.5	49 66	58.6	4.4	59.5	JUN			
JUL	20	84.6	2.6	85.0	90.5 60	80.5 55	I	102 67	95.9	3.3	96.0	55 66	67.6	5.7	68.5	JUL			
AUG	20	83.4	4.7	83.5	92.8 61	75.6 64	I	107 61	96.4	4.1	97.0	57 60	66.8	7.5	66.5	AUG			
SEP	20	74.9	5.1	74.0	83.9 67	66.4 65	I	98 67	89.1	4.9	89.5	47 56	55.9	5.2	56.0	SEP			
OCT	5	60.9	4.2	61.0	66.2 63 M	55.1 69	I	87 57	78.6	6.2	78.0	44 70	46.2	2.5	46.0	OCT			

MINIMUM DAILY TEMPERATURE

STATION NUMBER 100409 KINGSTON RS 10-DAY AND MONTHLY PERIOD MEANS										1951-1970 10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR		HIGH,YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW,YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS			
MAY 1	9	35.4	3.1	35.0	40.7 66	30.7 68 M	I	48 66	42.2	3.9	43.0	25 67	29.1	2.8	30.0	MAY 1			
MAY 11	9	37.3	2.3	37.0	40.5 69 M	34.5 66	I	52 70	45.0	4.2	45.0	26 66	30.1	3.6	30.0	MAY 11			
MAY 21	11	40.1	2.3	40.0	43.2 61	36.5 51	I	52 69	49.4	2.7	50.0	26 66	31.0	4.0	32.0	MAY 21			
JUN 1	19	44.1	3.8	44.0	50.0 57	37.4 51	I	60 52	52.1	4.3	53.0	28 51	36.3	3.7	37.0	JUN 1			
JUN 11	19	44.3	2.6	43.0	49.5 63	39.3 54	I	59 63	52.1	3.1	52.0	31 54	36.3	3.6	36.0	JUN 11			
JUN 21	19	44.0	3.4	44.0	50.8 70	36.9 53 M	I	63 70	52.1	4.8	52.0	28 53	35.5	3.8	35.0	JUN 21			
JUL 1	19	45.3	3.0	45.0	51.2 70	38.7 62	I	60 54	53.1	3.6	54.0	31 62	38.4	3.5	39.0	JUL 1			
JUL 11	19	47.1	2.7	46.0	51.5 70	39.7 62	I	60 67	54.5	3.5	55.0	33 62	40.4	3.1	41.0	JUL 11			
JUL 21	19	45.6	3.2	46.0	50.8 55	39.5 54	I	73 55	54.3	7.6	52.0	33 54	38.6	3.3	39.0	JUL 21			
AUG 1	19	45.7	3.1	46.0	51.8 65	40.6 69	I	62 65	53.6	5.5	53.0	32 54	39.5	3.5	40.0	AUG 1			
AUG 11	19	44.8	2.8	45.0	49.2 65	40.9 52	I	62 65	52.9	4.9	52.0	33 69	38.4	2.8	38.0	AUG 11			
AUG 21	19	44.4	2.7	44.0	47.9 61	38.0 55	I	61 67	52.4	4.6	53.0	30 59	36.4	3.7	37.0	AUG 21			
SEP 1	20	41.8	3.1	41.5	48.7 67	36.1 56	I	63 67	50.6	4.5	50.0	25 56	34.3	4.6	35.0	SEP 1			
SEP 11	19	40.4	3.8	40.0	47.3 59	32.5 60	I	57 59	49.3	3.8	49.0	22 70	32.5	5.5	34.0	SEP 11			
SEP 21	20	39.1	3.8	38.5	45.0 63	30.9 61	I	60 67	48.4	4.5	47.5	24 70	31.0	5.2	31.5	SEP 21			
OCT 1	9	36.3	2.2	36.0	39.4 63 M	32.1 52 M	I	54 66	43.7	5.6	43.0	24 66	29.1	4.4	28.0	OCT 1			
OCT 11	7	34.2	4.1	35.0	38.9 65 M	27.8 69	I	50 67	43.0	3.7	42.0	22 70	26.0	4.3	26.0	OCT 11			
OCT 21	5	34.4	3.8	35.0	37.3 66 M	27.8 70	I	50 63	42.2	6.5	43.0	23 70	26.8	3.3	28.0	OCT 21			
MONTH																			
MAY	8	38.0	1.2	38.0	39.7 69 M	35.9 65	I	52 70	50.9	2.1	52.0	25 67	27.5	2.1	26.5	MAY			
JUN	19	44.1	2.5	44.0	48.6 58	40.6 51 M	I	63 70	54.7	3.8	54.0	28 53	33.6	3.4	34.0	JUN			
JUL	18	46.2	1.8	45.5	50.5 70	42.7 53 M	I	73 55	57.9	5.0	56.0	31 62	36.7	2.3	37.0	JUL			
AUG	19	45.0	2.2	45.0	49.2 65	40.1 55	I	62 65	56.7	3.9	57.0	30 59	35.4	3.2	36.0	AUG			
SEP	19	40.5	2.9	40.0	45.4 63	34.8 61	I	63 67	52.4	4.2	52.0	22 70	28.0	4.6	26.0	SEP			
OCT	5	34.7	2.4	34.0	37.1 63 M	31.2 70	I	54 66	47.8	4.6	48.0	22 70	23.2	1.8	22.0	OCT			

(con.)

Table 9 (Con.)

MAXIMUM DAILY TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100412 MAGEE RS										1963-1972									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.		STD.		HIGHEST	LOWEST					STD.		HIGHEST	LOWEST					
BEGINS	YRS	MEAN	DEV.	MEDIAN	AVG.YR	AVG.YR		HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW		PRD.	BEGINS	
JUN 1	8	72.7	6.4	73.0	80.0	70	64.4	71	82.0	6.7	82.0	48.66	60.5	8.5	62.0		JUN 1		
JUN 11	9	70.6	5.0	68.0	79.7	69	66.1	71	83.0	5.6	85.0	50.72	57.9	6.1	57.0		JUN 11		
JUN 21	9	71.8	5.5	71.0	80.1	70	61.8	69	83.7	4.4	85.0	51.69	57.9	5.6	57.0		JUN 21		
JUL 1	9	80.0	5.9	81.0	89.2	68	71.1	71	87.7	5.6	88.0	54.66	67.0	8.2	70.0		JUL 1		
JUL 11	10	81.2	4.7	82.0	87.0	67	71.9	72	90.6	5.5	90.5	60.72	69.0	5.4	69.0		JUL 11		
JUL 21	10	82.8	3.3	83.0	87.4	71	76.2	70	90.0	2.7	90.0	64.65	72.2	6.8	72.5		JUL 21		
AUG 1	10	85.2	5.0	84.5	92.5	71	74.6	64	91.4	4.7	93.0	62.64	75.8	7.3	75.5		AUG 1		
AUG 11	10	82.1	7.0	82.0	95.1	67	68.7	68	89.3	5.4	87.5	54.68	71.8	11.6	71.5		AUG 11		
AUG 21	10	78.6	7.4	80.0	86.6	70	67.1	65	88.8	6.9	91.5	55.64	66.6	8.6	67.0		AUG 21		
SEP 1	10	75.5	8.0	74.5	87.3	63	65.6	64	84.8	7.6	86.5	50.71	62.4	9.8	61.0		SEP 1		
SEP 11	10	67.9	6.8	67.5	78.5	67	56.8	65	78.6	7.1	79.0	45.65	55.9	7.0	56.0		SEP 11		
SEP 21	7	71.1	9.2	66.0	83.5	67	60.3	71	82.0	6.8	80.0	47.68	59.7	10.6	55.0		SEP 21		
MONTH										MONTH									
JUN	8	71.2	2.6	71.0	75.6	70	67.4	71	87.3	2.1	87.0	48.66	51.9	2.6	51.5		JUN		
JUL	9	81.5	2.2	82.0	84.5	67	77.1	72	92.9	3.6	93.0	54.66	62.9	5.3	64.0		JUL		
AUG	10	81.8	5.2	82.5	88.7	67	72.9	64	93.8	3.5	95.0	54.68	64.1	7.2	67.0		AUG		
SEP	7	72.6	7.6	72.0	82.7	67	64.5	70	87.4	6.6	88.0	45.65	53.6	4.8	52.0		SEP		

MINIMUM DAILY TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100412										MAGEE RS		1963-1972									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES											
PRO. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG. YR	LOWEST AVG. YR		HIGH. YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW. YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRO. BEGINS					
JUN 1	8	41.4	2.6	41.0	45.0 64	36.0 65	I	56 72	49.3	4.8	49.5	30 68	33.8	2.8	33.5	JUN 1					
JUN 11	9	41.3	3.3	41.0	44.9 65	35.3 69	I	52 67	48.3	2.7	48.0	28 69	34.3	3.6	34.0	JUN 11					
JUN 21	9	41.6	1.9	41.0	45.2 70	39.5 64	I	57 70	50.3	3.8	49.0	30 68	34.0	2.2	34.0	JUN 21					
JUL 1	9	41.3	3.3	42.0	45.2 64	35.0 67	I	54 72	49.0	3.8	49.0	30 72	35.6	3.2	37.0	JUL 1					
JUL 11	10	41.6	4.0	41.0	48.0 70	35.5 69	I	56 72	51.7	4.4	53.0	29 69	35.0	4.6	34.0	JUL 11					
JUL 21	10	40.3	4.7	38.5	46.8 65	35.0 63	I	60 64	48.5	6.5	47.0	29 69	34.1	4.4	33.5	JUL 21					
AUG 1	10	40.5	6.0	40.0	49.0 65	32.5 69	I	60 65	48.1	7.1	49.0	28 67	34.2	5.3	33.0	AUG 1					
AUG 11	10	39.6	5.3	39.5	46.8 64	32.4 67	I	59 65	48.8	8.2	50.5	26 68	32.1	4.8	31.5	AUG 11					
AUG 21	10	39.7	5.2	41.0	45.9 65	32.5 67	I	55 66	49.8	4.4	49.5	23 67	31.2	5.1	30.5	AUG 21					
SEP 1	10	39.0	2.7	38.5	42.8 71	35.2 69	I	56 67	47.7	4.4	46.5	28 69	31.5	3.0	31.0	SEP 1					
SEP 11	10	35.5	3.9	36.5	40.3 66	28.0 70	I	53 63	45.2	3.1	44.5	16 70	26.0	6.0	29.5	SEP 11					
SEP 21	7	35.7	5.0	33.0	43.4 69	30.3 70	I	50 66	45.0	3.8	46.0	20 70	26.9	6.1	26.0	SEP 21					
MONTH																					
JUN	8	41.3	1.2	40.5	43.0 64	40.1 68	I	57 70	52.8	3.0	52.0	28 69	31.9	2.2	33.0	JUN					
JUL	9	41.4	3.2	41.0	45.8 70	37.8 67	I	60 64	54.3	3.0	54.0	29 69	32.6	2.6	33.0	JUL					
AUG	10	39.9	4.7	39.5	46.4 65	32.7 67	I	60 65	53.5	4.2	54.0	23 67	29.4	4.1	29.5	AUG					
SEP	7	36.9	2.4	37.0	39.8 64	33.5 70	I	56 67	50.3	3.6	50.0	16 70	23.3	5.2	24.0	SEP					

Table 10--Frequency distribution of daily maximum and minimum temperatures for indicated years of record. Based on 24-hour periods noted for table 9

MAXIMUM DAILY TEMPERATURE										PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED															
STATION		DECEPTION CREEK HQ										1936-1945													
		TEMPERATURE VALUES																							
PRD. BEGINS	BELOW 0	0 TO 4	5 TO 9	10 TO 14	15 TO 19	20 TO 24	25 TO 29	30 TO 34	35 TO 39	40 TO 44	45 TO 49	50 TO 54	55 TO 59	60 TO 64	65 TO 69	70 TO 74	75 TO 79	80 TO 84	85 TO 89	90 TO 94	95 TO 99	100 AND ABOVE	PRD. BEGINS		
MAY 1											68	182	136	170	239	102	68	34					MAY 1		
MAY 11											67	144	167	244	144	100	89	22					MAY 11		
MAY 21										9		45	100	136	236	136	209	91	27		9		MAY 21		
JUN 1											20	20	100	170	330	200	90	60	10				JUN 1		
JUN 11												20	110	210	180	220	120	70	40	30			JUN 11		
JUN 21												40		111	61	192	162	242	141	40	10		JUN 21		
JUL 1													20	50	130	240	280	190	90		10		JUL 1		
JUL 11													10	60	120	140	230	220	170	50			JUL 11		
JUL 21														18		82	173	236	345	91	55		JUL 21		
AUG 1												10		60	110	250	190	310	70				AUG 1		
AUG 11														30	40	70	290	340	170	60			AUG 11		
AUG 21												9	9	36	173	145	182	245	155	45			AUG 21		
SEP 1												20	82	112	163	133	194	133	133	31			SEP 1		
SEP 11										11	11	111	156	67	156	100	144	111	111	22			SEP 11		
SEP 21												33	89	133	233	244	156	78	33				SEP 21		
OCT 1											11	100	211	200	189	122	89	56	22				OCT 1		
OCT 11											33	89	311	256	189	111	11						OCT 11		
OCT 21										71	172	202	263	202	91								OCT 21		
MONTH																MONTH									
MAY										3	42	118	132	181	208	115	128	52	17	3			MAY		
JUN											7	13	84	164	191	204	124	124	64	23	3		JUN		
JUL														16	35	110	184	248	255	116	35		JUL		
AUG												3	6	23	94	110	239	258	210	58			AUG		
SEP											4	54	108	104	183	158	165	108	94	18			SEP		
OCT									25	75	133	262	219	154	75	32	18	7					OCT		

MINIMUM DAILY TEMPERATURE										PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																
STATION		DECEPTION CREEK HQ										1936-1945														
		TEMPERATURE VALUES																								
PRD. BEGINS	BELOW 0	0 TO 4	5 TO 9	10 TO 14	15 TO 19	20 TO 24	25 TO 29	30 TO 34	35 TO 39	40 TO 44	45 TO 49	50 TO 54	55 TO 59	60 TO 64	65 TO 69	70 TO 74	75 TO 79	80 TO 84	85 TO 89	90 TO 94	95 TO 99	100 AND ABOVE	PRD. BEGINS			
MAY 1						80	307	330	227	45		11											MAY 1			
MAY 11						33	178	289	289	167	33	11											MAY 11			
MAY 21							118	127	327	236	136	55											MAY 21			
JUN 1							60	120	280	360	170	10											JUN 1			
JUN 11								90	200	420	250	40											JUN 11			
JUN 21						10	71	202	303	303	101	10											JUN 21			
JUL 1								30	200	370	240	150	10										JUL 1			
JUL 11								50	170	220	370	170	20										JUL 11			
JUL 21								18	136	400	318	82	45										JUL 21			
AUG 1							10	110	330	300	170	70	10										AUG 1			
AUG 11							20	130	340	250	140	110	10										AUG 11			
AUG 21							27	109	409	282	155	18											AUG 21			
SEP 1							41	133	245	306	194	82											SEP 1			
SEP 11						11	89	222	256	211	189	22											SEP 11			
SEP 21						22	156	344	178	167	111	22											SEP 21			
OCT 1							122	300	289	211	78												OCT 1			
OCT 11						78	111	378	200	211	11	11											OCT 11			
OCT 21					30	111	212	293	232	111	10												OCT 21			
MONTH																							MONTH			
MAY						35	194	240	285	156	63	28											MAY			
JUN							23	94	227	361	241	50	3										JUN			
JUL								32	168	332	310	132	26										JUL			
AUG								19	116	361	277	155	65	6									AUG			
SEP							11	94	230	227	230	165	43										SEP			
OCT					11	65	151	323	240	176	32	4											OCT			

(con.)

Table 10 (Con.)

MAXIMUM DAILY TEMPERATURE										PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																															
STATION NUMBER		101956										COVER D'ALENE										TEMPERATURE VALUES										1931-1980									
PRD. BEGINS	BELOW 0	0 TO 4	5 TO 9	10 TO 14	15 TO 19	20 TO 24	25 TO 29	30 TO 34	35 TO 39	40 TO 44	45 TO 49	50 TO 54	55 TO 59	60 TO 64	65 TO 69	70 TO 74	75 TO 79	80 TO 84	85 TO 89	90 TO 94	95 TO 99	100 AND ABOVE	PRD. BEGINS																		
JAN 1				14	53	70	86	240	279	186	55	10	6											JAN 1																	
JAN 11		2	16	14	31	74	76	179	308	185	101	14												JAN 11																	
JAN 21		4	6	20	61	65	89	181	253	201	97	20	2											JAN 21																	
FEB 1	2	4	4	10	14	26	56	130	274	292	140	44	4											FEB 1																	
FEB 11			4	12	12	6	26	76	252	358	156	72	26											FEB 11																	
FEB 21						10	17	46	182	344	225	121	51	5										FEB 21																	
MAR 1						4	12	50	185	293	219	143	68	14	12									MAR 1																	
MAR 11							4	10	58	282	296	164	104	46	32	4								MAR 11																	
MAR 21								22	46	153	241	210	150	108	51	20								MAR 21																	
APR 1							2	2	16	59	170	244	192	162	83	61	6	4						APR 1																	
APR 11									4	32	112	216	184	150	130	106	44	20						APR 11																	
APR 21									2	14	74	138	213	190	153	97	74	21	17	6				APR 21																	
MAY 1											29	100	157	176	172	166	108	67	18	6				MAY 1																	
MAY 11									2	10	51	106	167	196	153	182	76	43	14					MAY 11																	
MAY 21											33	82	134	187	176	165	121	74	24	4				MAY 21																	
JUN 1										2	8	44	107	139	207	211	149	95	36	2				JUN 1																	
JUN 11											2	30	91	157	171	219	167	89	62	12				JUN 11																	
JUN 21											2	18	64	108	184	188	198	136	74	20	6			JUN 21																	
JUL 1												2	18	48	112	158	218	234	142	58	8			JUL 1																	
JUL 11													2	16	80	122	187	217	199	137	40			JUL 11																	
JUL 21												2	2	16	31	47	142	263	276	182	38			JUL 21																	
AUG 1													6	16	38	106	154	222	276	148	34			AUG 1																	
AUG 11												2	14	26	56	76	197	229	215	137	48			AUG 11																	
AUG 21												11	35	70	116	149	180	202	134	79	24			AUG 21																	
SEP 1											4	16	41	98	142	161	197	179	120	39	4			SEP 1																	
SEP 11										6	10	46	145	139	125	161	179	123	56	10				SEP 11																	
SEP 21										4	4	41	71	149	182	133	155	141	98	22				SEP 21																	
OCT 1									2	4	19	91	136	171	153	169	153	79	23					OCT 1																	
OCT 11								2	10	37	141	214	216	227	114	31	4	2						OCT 11																	
OCT 21						2	2	4	15	56	156	257	205	182	81	41								OCT 21																	
NOV 1						4	4	25	80	150	277	285	140	25	10	4								NOV 1																	
NOV 11				4	2	6	14	39	148	333	256	152	41	4										NOV 11																	
NOV 21						8	26	103	263	297	196	81	26											NOV 21																	
DEC 1				8	8	6	49	196	284	216	163	59	10											DEC 1																	
DEC 11		2	2	18	38	84	208	280	206	136	26													DEC 11																	
DEC 21	2	2	4	2	15	31	88	221	300	215	87	31		2										DEC 21																	
MONTH																									MONTH																
JAN		2	7	17	49	69	84	199	279	191	85	15	3											JAN																	
FEB	1	1	3	8	9	14	34	86	239	331	171	76	25	1										FEB																	
MAR						1	5	27	94	240	252	173	109	58	32	8								MAR																	
APR							1	1	7	35	119	200	196	167	122	88	41	15	5	2				APR																	
MAY											1	13	61	114	158	185	165	152	89	46	15	1		MAY																	
JUN												1	4	31	87	135	188	206	171	106	58	11	2	JUN																	
JUL														1	7	27	73	107	181	239	208	128	29	JUL																	
AUG													5	19	38	71	112	177	217	206	120	35		AUG																	
SEP						1	1	1	7	25	73	166	186	112	139	133	159	172	133	66	16	1		SEP																	
OCT														190	151	106	59	27	8					OCT																	
NOV				1	1	5	15	56	164	261	243	172	69	9	3	1								NOV																	
DEC	1	1	2	3	14	25	74	209	288	213	127	38	3	1										DEC																	

(con.)

Table 10 (Con.)

MINIMUM DAILY TEMPERATURE											PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																																							
STATION NUMBER		101956										COUER D'ALENE										TEMPERATURE VALUES																			1931-1980									
PRD. BEGINS	BELOW 0	0 TO 4	5 TO 9	10 TO 14	15 TO 19	20 TO 24	25 TO 29	30 TO 34	35 TO 39	40 TO 44	45 TO 49	50 TO 54	55 TO 59	60 TO 64	65 TO 69	70 TO 74	75 TO 79	80 TO 84	85 TO 89	90 TO 94	95 TO 99	100 AND ABOVE	PRD. BEGINS																											
JAN 1	76	43	47	84	74	133	237	256	49	2														JAN 1																										
JAN 11	72	39	49	76	91	111	239	253	60	8	2													JAN 11																										
JAN 21	90	41	86	65	119	116	200	229	47	4	4													JAN 21																										
FEB 1	58	32	40	52	90	170	254	240	60	4														FEB 1																										
FEB 11	34	24	22	58	108	152	252	292	54	4														FEB 11																										
FEB 21	7	19	19	51	87	184	230	334	61	7														FEB 21																										
MAR 1	16	8	20	46	102	191	261	257	90	6														MAR 1																										
MAR 11	4	2		18	20	56	116	332	328	108	16													MAR 11																										
MAR 21			5	15	40	78	303	354	172	31	2													MAR 21																										
APR 1			2	4	12	73	240	361	212	85	12													APR 1																										
APR 11					2	34	176	353	275	136	24													APR 11																										
APR 21					2	8	102	266	339	197	77	8												APR 21																										
MAY 1						4	47	178	325	286	133	27												MAY 1																										
MAY 11							20	120	278	324	176	65	16											MAY 11																										
MAY 21						2	4	61	189	328	256	108	46	6										MAY 21																										
JUN 1							2	12	102	280	302	218	70	12	2									JUN 1																										
JUN 11							2	8	56	205	324	294	89	18	4									JUN 11																										
JUN 21								2	34	152	335	297	136	42	2									JUN 21																										
JUL 1									24	129	271	303	217	54	2									JUL 1																										
JUL 11									6	64	187	368	272	82	18	2								JUL 11																										
JUL 21									11	35	184	349	288	108	26									JUL 21																										
AUG 1									12	86	182	384	232	90	12	2								AUG 1																										
AUG 11								4	18	84	255	357	213	54	14									AUG 11																										
AUG 21									26	147	290	347	165	22	2									AUG 21																										
SEP 1								16	87	233	290	270	83	20										SEP 1																										
SEP 11						2	10	56	145	245	334	155	52											SEP 11																										
SEP 21						2	22	145	198	290	224	100	16	2										SEP 21																										
OCT 1						4	38	180	271	319	146	38	4											OCT 1																										
OCT 11					2	19	100	201	282	236	140	17	2											OCT 11																										
OCT 21		2		2	4	23	158	250	278	211	64	9												OCT 21																										
NOV 1		6	4	11	27	78	201	316	234	96	31													NOV 1																										
NOV 11	10	4	4	18	53	98	185	341	217	67	2													NOV 11																										
NOV 21		14	6	16	81	137	255	297	149	42	2													NOV 21																										
DEC 1		4	16	18	73	129	251	353	110	22	4													DEC 1																										
DEC 11	18	14	36	58	88	142	232	293	104	14														DEC 11																										
DEC 21	15	18	27	62	104	151	270	250	78	18	5													DEC 21																										
MONTH																									MONTH																									
JAN	79	41	62	75	95	120	224	246	52	5	2													JAN																										
FEB	35	25	28	54	96	168	246	286	58	5														FEB																										
MAR	6	3	14	27	65	127	299	314	125	18	1													MAR																										
APR						38	173	327	275	139	38	3												APR																										
MAY			1	1	5	38	173	327	275	139	38	3												MAY																										
JUN						2	23	118	262	314	190	68	22	2										JUN																										
JUL							1	7	64	213	320	269	98	24	3									JUL																										
AUG									1	19	107	244	363	202	54	16	9	1						AUG																										
SEP					1	11	72	143	256	283	175	51	7											SEP																										
OCT		1		1	2	16	101	212	277	254	115	21	2											OCT																										
NOV	3	8	5	14	54	104	214	318	200	68	12													NOV																										
DEC	12	16	27	47	89	141	252	297	97	18	3													DEC																										

(con.)

Table 10 (Con.)

MAXIMUM DAILY TEMPERATURE										PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																			
STATION NUMBER 100304 FERNAN RS										1951-1970																			
										TEMPERATURE VALUES																			
PRD. BEGINS	BELOW 0	0 4	5 9	10 14	15 19	20 24	25 29	30 34	35 39	40 44	45 49	50 54	55 59	60 64	65 69	70 74	75 79	80 84	85 89	90 94	95 99	100 AND ABOVE	PRD. BEGINS						
MAY 1											14	136	193	171	121	150	107	64	36	7			MAY 1						
MAY 11										6	6	44	81	156	206	119	256	81	38	6			MAY 11						
MAY 21												37	80	86	225	160	176	144	59	32			MAY 21						
JUN 1											5		42	95	126	216	200	174	84	53	5		JUN 1						
JUN 11													21	111	126	158	221	189	105	68			JUN 11						
JUN 21													10	60	120	205	205	215	90	70	25		JUN 21						
JUL 1													5	10	55	105	160	180	230	155	100		JUL 1						
JUL 11															5	45	95	170	265	215	170	35	JUL 11						
JUL 21															18	32	50	141	227	305	205	23	JUL 21						
AUG 1															5	15	30	95	170	205	300	150	30	AUG 1					
AUG 11															20	25	35	70	195	225	230	145	55	AUG 11					
AUG 21															18	41	95	127	186	159	159	73	100	41	AUG 21				
SEP 1															10	20	65	175	155	225	170	140	35	5	SEP 1				
SEP 11															5	35	126	156	111	141	201	171	45	10	SEP 11				
SEP 21															5	25	70	156	211	116	176	95	116	30	SEP 21				
OCT 1															6	28	89	162	123	140	184	179			OCT 1				
OCT 11																		38	191	261	185	204	76		OCT 11				
OCT 21																									OCT 21				
									7	7	64	121	200	186	221	93	100												
MONTH																													
MAY											2	6	68	113	133	189	144	183	101	45	16			MAY					
JUN											2			24	88	124	193	209	193	93	64	10		JUN					
JUL														2	3	26	60	100	163	240	227	160	19	JUL					
AUG															6	23	47	66	119	174	195	197	131	42	AUG				
SEP																								SEP					
OCT									2	2	21	59	155	202	172	147	124	82	34					OCT					

MINIMUM DAILY TEMPERATURE										PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																			
STATION NUMBER 100304 FERNAN RS										1951-1970																			
										TEMPERATURE VALUES																			
PRD. BEGINS	BELOW 0	0 4	5 9	10 14	15 19	20 24	25 29	30 34	35 39	40 44	45 49	50 54	55 59	60 64	65 69	70 74	75 79	80 84	85 89	90 94	95 99	100 AND ABOVE	PRD. BEGINS						
MAY 1						14	29	193	343	264	143	14											MAY 1						
MAY 11							6	125	263	331	200	69	6										MAY 11						
MAY 21							5	53	155	337	289	118	32	11									MAY 21						
JUN 1							5	5	100	268	247	295	68	5	5								JUN 1						
JUN 11									11	47	232	311	316	63	11	11							JUN 11						
JUN 21									5	25	165	390	285	90	40								JUN 21						
JUL 1										20	145	300	330	140	65								JUL 1						
JUL 11											50	160	395	280	105	10							JUL 11						
JUL 21											14	41	182	359	273	114	18						JUL 21						
AUG 1											5	85	165	405	230	105							AUG 1						
AUG 11												55	285	375	195	65	25						AUG 11						
AUG 21																							AUG 21						
SEP 1												14	141	282	355	177	27	5					SEP 1						
SEP 11												15	115	220	285	280	60	25					SEP 11						
SEP 21												20	40	106	256	362	156	60					SEP 21						
OCT 1												15	111	176	291	266	116	15	10				OCT 1						
OCT 11												17	190	274	318	151	39	11					OCT 11						
OCT 21																							OCT 21						
						14	107	286	321	193	71	7																	
MONTH																													
MAY						4	12	117	244	314	218	72	14	4									MAY						
JUN							2	7	57	221	317	298	74	19	5								JUN						
JUL									11	77	213	361	232	95	10								JUL						
AUG									6	95	245	377	200	65	10	2							AUG						
SEP									12	55	132	256	304	184	45	12							SEP						
OCT						4	74	233	269	273	124	19	4										OCT						

MINIMUM DAILY TEMPERATURE										PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																			
STATION NUMBER 100304 FERNAN RS										1951-1970																			
										TEMPERATURE VALUES																			
PRD. BEGINS	BELOW 0	0 4	5 9	10 14	15 19	20 24	25 29	30 34	35 39	40 44	45 49	50 54	55 59	60 64	65 69	70 74	75 79	80 84	85 89	90 94	95 99	100 AND ABOVE	PRD. BEGINS						
MAY 1						14	29	193	343	264	143	14												MAY 1					
MAY 11							6	125	263	331	200	69	6											MAY 11					
MAY 21							5	53	155	337	289	118	32	11										MAY 21					
JUN 1							5	5	100	268	247	295	68	5										JUN 1					
JUN 11								11	47	232	311	316	63	11	11									JUN 11					
JUN 21								5	25	165	390	285	90	40										JUN 21					
JUL 1								20	145	300	330	140	65											JUL 1					
JUL 11										50	160	395	280	105	10									JUL 11					
JUL 21									14	41	182	359	273	114	18									JUL 21					
AUG 1									5	85	165	405	230	105		5								AUG 1					
AUG 11										55	285	375	195	65	25									AUG 11					
AUG 21										14	141	282	355	177	27	5								AUG 21					
SEP 1									15	115	220	285	280	60	25									SEP 1					
SEP 11							20	40	106	256	362	156	60											SEP 11					
SEP 21							15	111	176	291	266	116	15	10										SEP 21					
OCT 1							17	190	274	318	151	39	11											OCT 1					
OCT 11								108	236	217	293	140	6											OCT 11					
OCT 21						14	107	286	321	193	71	7												OCT 21					
MONTH																													
MAY						4	12	117	244	314	218	72	14	4										MAY					
JUN							2	7	57	221	317	298	74	19	5									JUN					
JUL									11	77	213	361	232	95	10									JUL					
AUG									5	95	245	377	200	65	10	2								AUG					
SEP								12	55	132	256	304	184	45	12									SEP					
OCT						4	74	233	269	273	124	19	4											OCT					

(con.)

Table 10 (Con.)

MAXIMUM DAILY TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100409		KINGSTON RS																		1951-1970										
		TEMPERATURE VALUES																														
PRD.	BELOW	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	AND	PRD.								
BEGINS	0	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99	ABOVE		BEGINS								
MAY 1										24	37	183	220	122	110	134	98	24	24					MAY 1								
MAY 11										11		88	22	198	198	165	253	55	11					MAY 11								
MAY 21												16	71	142	150	165	213	197	47					MAY 21								
JUN 1											5		35	80	186	191	241	136	101	25				JUN 1								
JUN 11												10	35	105	125	175	200	185	110	45	10			JUN 11								
JUN 21												5	15	81	146	217	197	172	96	61	10			JUN 21								
JUL 1													10	15	60	150	140	250	185	145	45			JUL 1								
JUL 11															5	10	55	140	190	260	190	130	20	JUL 11								
JUL 21																18	45	73	168	318	295	73	9	JUL 21								
AUG 1															10	25	150	190	270	270	55	20		AUG 1								
AUG 11													5	25	35	25	115	190	290	170	135	10		AUG 11								
AUG 21													32	41	114	127	191	177	145	82	86	5		AUG 21								
SEP 1													15	50	100	155	175	195	170	135	5			SEP 1								
SEP 11											5	10	66	141	121	141	152	192	141	20	10			SEP 11								
SEP 21											10	45	71	141	197	136	146	81	131	40				SEP 21								
OCT 1											84	74	147	137	126	105	211	95	21					OCT 1								
OCT 11											33	217	267	200	100	83	100							OCT 11								
OCT 21										49	131	295	164	148	148	66								OCT 21								
MONTH																										MONTH						
MAY										10	10	83	97	153	153	157	193	107	30	7					MAY							
JUN											2	5	28	89	152	194	213	164	102	44	7			JUN								
JUL													3	6	29	82	116	202	256	213	82	10		JUL								
AUG													13	26	55	61	153	185	232	171	92	11		AUG								
SEP											5	18	50	111	139	144	158	156	148	65	5			SEP								
OCT										14	83	176	185	157	125	88	120	42	9					OCT								

MINIMUM DAILY TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100409		KINGSTON RS																		1951-1970											
		TEMPERATURE VALUES																															
PRD.	BELOW	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100		PRD.									
BEGINS	0	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99	AND ABOVE		BEGINS									
MAY 1							134	244	415	159	49													MAY 1									
MAY 11							44	231	451	165	77	33											MAY 11										
MAY 21							55	118	244	370	134	79											MAY 21										
JUN 1							5	43	199	290	258	183	27	5									JUN 1										
JUN 11								42	201	238	344	153	21										JUN 11										
JUN 21							16	37	171	283	305	134	43	11									JUN 21										
JUL 1								21	116	349	265	185	58	5									JUL 1										
JUL 11								10	61	255	357	219	87	10									JUL 11										
JUL 21								9	113	349	302	165	33	24		5							JUL 21										
AUG 1								5	94	354	339	135	52	21									AUG 1										
AUG 11								5	137	384	284	132	53	5									AUG 11										
AUG 21								52	160	258	357	131	38	5									AUG 21										
SEP 1							20	90	246	317	221	75	25	5									SEP 1										
SEP 11						15	52	68	289	268	232	46	10										SEP 11										
SEP 21						15	86	157	212	283	207	35		5									SEP 21										
OCT 1						43	96	170	404	170	85	32											OCT 1										
OCT 11						150	133	183	317	183	17	17											OCT 11										
OCT 21						67	167	267	233	250		17											OCT 21										
MONTH																																MONTH	
MAY							73	187	353	250	93	43											MAY										
JUN							7	41	190	267	302	157	30	5									JUN										
JUL								13	97	318	308	189	59	13		2							JUL										
AUG								22	131	329	328	133	47	10									AUG										
SEP						10	52	112	249	289	220	52	12	3									SEP										
OCT						79	126	201	332	196	42	23											OCT										

Table 11--Afternoon dry bulb temperature (degrees Fahrenheit) and relative humidity (percent) statistics for fire season; data observed mostly near 1500 P.s.t. (1630 at Deception Creek), for indicated years of record. Daily minimum relative humidity is included for Deception Creek. Separate summary of Fernan Ranger Station 1974-84 data, at present 1200 observation time, is included for comparison (see text). Letter "M" in table denotes occurrence of missing data (see table 9 caption)

DRY BULB TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION			DECEPTION CREEK HQ										1936-1945										
			10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES										
PRD.	NO.		MEAN	STD.		HIGHEST		LOWEST			HIGH.YR	AVG.		STD.	MEDIAN		LOW.YR	AVG.		STD.	MEDIAN		PRD.
BEGINS	YRS			DEV.		AVG.YR		AVG.YR				HIGH		DEV.	HIGH			LOW		DEV.	LOW		BEGINS
MAY	1	9	52.5	5.8	52.0	62.0 40	45.3 43				76 40	63.6	9.4	61.0			35 43	42.8	4.7	43.0		MAY 1	
MAY	11	9	55.8	5.7	53.0	65.2 44	48.9 45				76 41	66.3	7.2	67.0			35 36	45.7	7.4	45.0		MAY 11	
MAY	21	10	63.6	4.2	62.0	70.2 40	59.1 44				82 44	76.0	4.4	76.0			39 44	50.5	5.6	51.0		MAY 21	
JUN	1	10	61.5	3.7	60.5	68.8 38	55.5 39				80 40	74.4	3.9	73.0			43 36	47.7	2.7	48.0		JUN 1	
JUN	11	10	64.0	6.5	62.5	79.2 40	57.2 43				90 40	75.4	7.3	72.5			45 45	51.7	7.6	50.0		JUN 11	
JUN	21	10	71.1	4.8	69.0	77.2 40	65.0 43				89 39	83.6	3.1	83.5			50 45	57.9	7.7	54.0		JUN 21	
JUL	1	10	75.4	4.6	75.5	81.5 42	69.1 38				90 41	84.9	3.3	84.5			53 38	66.1	8.4	66.5		JUL 1	
JUL	11	10	77.2	5.5	77.0	84.4 38	69.0 42				92 40	86.8	3.2	86.5			57 43	65.0	6.0	65.0		JUL 11	
JUL	21	10	78.3	3.8	78.5	82.8 39	70.9 40				92 38	86.3	3.1	86.0			55 40	66.8	7.8	66.5		JUL 21	
AUG	1	10	75.3	4.6	76.0	81.0 42	65.0 37				86 45	82.3	4.3	83.5			53 37	65.0	5.9	66.0		AUG 1	
AUG	11	10	73.3	5.5	74.0	81.1 40	65.2 38				88 40	80.1	4.8	80.5			50 38	63.7	7.8	64.5		AUG 11	
AUG	21	10	68.4	5.1	67.0	76.0 40	60.3 37				88 40	78.8	6.1	78.5			52 43	56.3	4.3	54.0		AUG 21	
SEP	1	10	63.7	4.3	63.0	68.9 40	55.0 41				83 38	72.6	7.3	74.5			49 41	53.8	3.3	53.5		SEP 1	
SEP	11	9	58.3	6.0	57.0	66.6 38	49.5 41				76 43	67.1	6.5	67.0			41 36	49.0	6.4	47.0		SEP 11	
SEP	21	9	56.2	4.6	55.0	62.4 38	48.9 37				70 38	63.3	5.3	64.0			43 37	49.7	5.1	48.0		SEP 21	
OCT	1	9	50.1	4.7	49.0	60.3 43	45.0 41				66 43	56.1	6.4	54.0			38 41	44.1	4.6	44.0		OCT 1	
OCT	11	9	46.8	4.2	46.0	54.1 40	41.1 43				61 40	52.2	4.5	52.0			33 43	40.8	5.8	43.0		OCT 11	
OCT	21	9	41.7	4.2	42.0	48.4 37	36.8 43				55 39	48.2	5.1	48.0			31 41	35.8	4.6	35.0		OCT 21	
MONTH																							MONTH
MAY		9	57.5	3.8	56.0	65.2 40	53.1 43				82 44	75.9	4.7	76.0			35 43	40.0	3.8	39.0		MAY	
JUN		10	65.5	4.0	64.5	73.3 40	60.8 43				90 40	84.0	3.7	83.5			43 36	47.0	2.8	47.0		JUN	
JUL		10	77.0	1.7	76.5	79.2 41	74.8 44				92 40	88.9	2.5	89.5			53 38	58.6	4.1	58.0		JUL	
AUG		10	72.2	4.2	71.0	78.4 40	64.1 37				88 40	83.0	4.4	83.5			50 38	55.2	4.4	54.0		AUG	
SEP		9	59.4	4.2	59.0	64.7 38	51.9 41				83 38	73.0	7.3	76.0			41 36	45.8	2.9	46.0		SEP	
OCT		9	46.2	1.8	45.0	49.2 40	44.5 39				66 43	57.9	5.4	57.0			31 41	35.3	4.4	34.0		OCT	

RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION		DECEPTION CREEK HQ										1936-1945									
		10-DAY AND MONTHLY PERIOD MEANS								10-DAY AND MONTHLY EXTREME DAILY VALUES											
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR			HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS				
MAY 1	9	64.3	11.7	67.0	80.1 36 M	44.4 44	I	100 43	89.4	14.9	93.0	28 44	42.1	14.2	36.0	MAY 1					
MAY 11	9	62.7	15.1	69.0	81.9 45	43.2 44	I	100 43	87.1	14.5	91.0	29 44	42.6	11.3	46.0	MAY 11					
MAY 21	10	53.2	9.7	51.5	69.7 42	38.9 40	I	100 42	84.7	11.3	85.0	22 44	30.2	8.2	29.5	MAY 21					
JUN 1	10	57.8	10.4	56.5	69.4 45	37.9 38	I	100 41	89.7	6.4	93.0	24 38	32.6	7.6	30.5	JUN 1					
JUN 11	10	57.9	12.1	59.0	71.3 39	30.3 40	I	100 42	85.0	16.8	88.5	22 45	33.0	7.0	32.0	JUN 11					
JUN 21	10	47.2	10.7	47.0	60.2 44	29.0 40	I	100 42	76.1	23.6	87.5	22 40	28.5	4.1	28.5	JUN 21					
JUL 1	10	43.3	8.0	42.5	55.9 38	32.2 45	I	100 39	69.8	16.8	67.0	21 45	27.4	3.4	27.5	JUL 1					
JUL 11	10	43.3	7.3	41.5	54.8 42	34.7 40	I	94 37	71.8	16.0	70.0	21 45	28.3	4.6	27.5	JUL 11					
JUL 21	10	41.6	8.6	43.0	52.5 40	29.9 45	I	100 41	68.4	22.4	63.0	21 45	28.2	5.8	29.0	JUL 21					
AUG 1	10	42.4	11.3	40.0	68.6 37	29.9 38	I	88 37	65.1	16.4	67.0	16 45	26.9	10.9	24.0	AUG 1					
AUG 11	10	46.9	10.1	48.0	58.8 44	31.8 40	I	94 44	69.9	19.0	72.0	21 45	28.4	6.3	27.0	AUG 11					
AUG 21	10	55.4	11.2	56.5	73.2 41	38.8 40	I	100 41	79.6	14.9	82.0	19 45	36.0	12.6	32.0	AUG 21					
SEP 1	10	66.2	8.8	61.5	81.9 37	57.1 39	I	100 41	90.8	8.3	94.0	25 45	38.1	12.4	34.5	SEP 1					
SEP 11	9	74.0	11.5	76.0	88.8 41	54.9 43	I	100 41	91.2	9.8	93.0	31 44	55.7	15.1	59.0	SEP 11					
SEP 21	9	75.7	9.2	76.0	86.7 44	63.6 38	I	100 41	88.0	9.0	87.0	45 43	59.9	12.2	55.0	SEP 21					
OCT 1	7	86.6	8.4	88.0	94.5 40	70.3 43	I	100 40	95.3	3.3	94.0	50 42	75.6	14.1	81.0	OCT 1					
OCT 11	8	91.8	1.5	91.0	94.1 37	90.0 38	I	100 43	98.3	3.2	100.0	76 39	83.8	5.6	85.5	OCT 11					
OCT 21	8	93.8	3.9	94.5	98.5 40	86.7 36 M	I	100 43	98.3	3.2	100.0	67 36	86.3	9.2	90.5	OCT 21					
MONTH																				MONTH	
MAY	9	59.9	8.6	63.0	71.3 42	46.3 40 M	I	100 43	95.9	3.9	93.0	22 44	30.7	7.5	30.0	MAY					
JUN	10	54.4	7.7	55.5	62.2 41	37.6 40	I	100 42	94.0	4.9	93.0	22 45	26.3	3.4	26.0	JUN					
JUL	10	42.7	4.5	43.5	48.1 37	32.9 45	I	100 41	88.9	11.4	91.5	21 45	25.1	2.8	26.0	JUL					
AUG	10	48.5	9.6	48.5	65.6 37	34.1 40	I	100 41	84.4	13.8	88.5	16 45	24.5	7.3	24.0	AUG					
SEP	9	72.1	8.5	72.0	84.0 41	59.1 43	I	100 41	94.7	4.6	94.0	25 45	37.8	12.2	34.0	SEP					
OCT	8	91.1	3.6	91.0	95.7 40	86.2 43	I	100 43	98.4	3.0	100.0	50 42	73.0	12.0	76.5	OCT					

(con.)

Table 11 (Con.)

MINIMUM RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION		DECEPTION CREEK HQ										1936-1945									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES											
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG. YR	LOWEST AVG. YR	I	HIGH, YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW, YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS					
MAY 1	7	39.9	11.0	39.0	55.3 42	22.6 45	I	99 42	65.0	20.7	60.0	14 45	22.1	4.7	23.0	MAY 1					
MAY 11	8	44.7	12.0	40.0	66.9 41	32.6 40	I	99 41	68.4	16.8	66.0	16 39	26.3	8.2	24.0	MAY 11					
MAY 21	9	42.6	9.8	38.0	59.6 42	31.4 40	I	99 42	75.2	14.9	75.0	13 45	21.9	6.2	21.0	MAY 21					
JUN 1	10	46.3	8.4	45.0	59.0 41	34.6 44	I	99 41	79.8	12.1	80.5	12 44	25.5	7.0	25.0	JUN 1					
JUN 11	10	45.3	12.4	48.0	60.8 43	25.7 40	I	93 37	70.5	19.8	76.0	16 45	26.9	8.1	26.0	JUN 11					
JUN 21	10	36.7	7.7	36.0	48.9 41	25.4 40	I	99 42	64.8	23.5	66.5	10 36	21.3	5.6	23.0	JUN 21					
JUL 1	10	32.2	7.1	32.0	40.9 39 M	16.8 45	I	68 39	45.7	14.0	44.0	11 45	21.8	4.3	22.5	JUL 1					
JUL 11	10	30.7	7.0	28.5	45.2 42	22.8 45	I	75 37	45.4	13.6	41.5	10 45	19.9	5.2	20.5	JUL 11					
JUL 21	10	31.2	8.3	28.5	49.1 40	20.5 36	I	99 40	51.6	21.1	45.5	13 36	19.5	4.1	19.0	JUL 21					
AUG 1	10	31.9	7.4	28.5	44.0 37	24.5 39	I	84 37	51.9	17.8	45.5	15 45	18.1	3.2	18.0	AUG 1					
AUG 11	10	31.3	6.8	28.5	44.6 38	23.9 40	I	88 38	49.4	18.3	44.5	14 45	20.8	4.5	20.0	AUG 11					
AUG 21	10	35.9	8.4	32.0	50.6 41	26.1 38	I	83 43	62.7	14.0	64.0	10 36	20.4	7.4	19.0	AUG 21					
SEP 1	10	45.5	12.6	41.0	72.9 41	26.7 44	I	99 41	80.9	11.7	82.0	15 44	24.5	9.4	22.0	SEP 1					
SEP 11	9	47.8	16.6	44.0	80.6 41	28.9 38	I	99 41	75.1	17.9	77.0	17 44	29.9	14.8	26.0	SEP 11					
SEP 21	9	43.8	10.1	42.0	65.6 40	30.6 36	I	99 40	64.3	17.7	60.0	21 36	31.7	6.8	30.0	SEP 21					
OCT 1	7	62.4	16.0	58.0	80.6 38	41.9 36	I	100 37	88.9	9.8	91.0	26 43	38.9	13.8	34.0	OCT 1					
OCT 11	8	69.2	9.1	72.0	75.3 40	47.6 36	I	100 37	85.3	10.9	86.5	28 36	45.6	10.8	47.0	OCT 11					
OCT 21	8	76.9	13.1	80.0	91.3 40	50.4 36 M	I	100 38	92.0	11.1	97.0	36 36	55.5	14.6	55.0	OCT 21					
MONTH																					
MAY	7	43.8	9.3	42.0	57.4 42	32.6 37	I	99 42	82.1	13.7	80.0	13 45	18.7	3.4	20.0	MAY					
JUN	10	42.8	7.1	41.5	52.5 41	32.3 40	I	99 42	84.3	11.2	85.0	10 36	20.2	5.8	21.0	JUN					
JUL	10	31.3	4.6	32.0	37.1 42	22.3 45	I	99 40	63.6	16.9	61.0	10 45	17.7	4.1	18.0	JUL					
AUG	10	33.1	6.0	31.0	44.7 41	26.2 39	I	88 38	70.2	13.8	72.5	10 36	17.1	4.3	17.0	AUG					
SEP	9	45.9	10.8	41.0	67.8 41	37.6 43	I	99 41	83.6	10.6	80.0	15 44	23.2	6.8	22.0	SEP					
OCT	8	70.3	11.4	73.0	82.3 40	46.6 36 M	I	100 38	94.6	6.8	97.0	26 43	37.4	11.8	33.0	OCT					

(con.)

Table 11 (Con.)

DRY HULB TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100304 FERNAN RS										1951-1970									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.																PRD.		
BEGINS	YRS	MEAN	STD.	MEDIAN	HIGHEST	LOWEST				STD.	MEDIAN						BEGINS		
			DEV.		AVG.YR	AVG.YR		HIGH.YR	AVG.	DEV.	HIGH		LOW.YR	AVG.	STD.	MEDIAN			
							I		HIGH					LOW	DEV.	LOW			
MAY	1	14	61.0	6.0	60.0	74.6 66	I	89 66	74.7	7.7	74.0		42 64	47.4	4.2	46.5	MAY		
MAY	11	16	64.8	5.1	65.0	71.3 54	I	89 54	78.8	5.8	77.0		39 55	50.1	6.4	50.5	MAY		
MAY	21	17	67.1	6.8	66.0	81.8 58	I	93 58	80.2	6.8	82.0		40 64	52.1	6.4	51.0	MAY		
JUN	1	19	69.6	6.3	68.0	80.5 69	I	93 70	81.7	5.8	82.0		45 66	55.6	8.2	54.0	JUN		
JUN	11	19	71.6	5.8	70.0	81.4 63	I	91 69	83.9	5.6	83.0		49 60	57.9	6.7	56.0	JUN		
JUN	21	20	72.4	5.3	71.5	81.0 61	I	96 58	84.3	5.9	84.0		50 55	59.3	5.4	59.5	JUN		
JUL	1	20	79.1	6.0	78.5	91.5 68	I	98 68	91.3	4.0	90.5		52 55	63.9	8.4	63.0	JUL		
JUL	11	20	84.0	5.0	83.0	94.9 60	I	101 67	94.2	4.3	94.5		64 63	73.1	6.6	71.5	JUL		
JUL	21	20	85.3	5.0	86.5	92.1 62	I	104 59	93.9	4.6	94.0		56 65	73.3	9.7	74.0	JUL		
AUG	1	20	83.7	5.7	84.0	91.9 61	I	107 61	93.5	5.9	94.5		59 64	71.7	7.8	73.0	AUG		
AUG	11	20	83.1	7.2	82.5	99.4 67	I	102 67	93.1	4.9	93.5		53 64	72.3	10.6	73.0	AUG		
AUG	21	20	76.5	7.5	75.0	89.3 70	I	102 67	90.4	8.2	89.0		52 60	63.1	8.7	62.0	AUG		
SEP	1	20	76.1	6.7	75.0	89.3 55	I	96 58	86.1	6.3	86.0		51 64	63.4	9.0	63.0	SEP		
SEP	11	20	70.3	6.5	71.5	78.9 56	I	91 59	83.1	6.7	85.5		44 57	54.8	6.3	55.0	SEP		
SEP	21	20	67.8	7.4	65.0	80.8 67	I	93 67	78.6	8.4	77.5		43 58	54.1	6.8	53.5	SEP		
OCT	1	18	62.3	5.8	61.5	74.1 52	I	84 63	74.5	5.8	74.5		40 58	49.9	7.3	49.5	OCT		
OCT	11	16	56.8	5.1	56.5	66.9 63	I	76 61	65.4	6.6	65.0		41 51	47.9	4.6	47.5	OCT		
OCT	21	13	52.1	6.2	53.0	64.5 65	I	71 69	63.1	6.0	64.0		27 57	42.7	7.8	41.0	OCT		
MONTH										MONTH									
MAY	16	64.2	3.7	63.5	68.9 69	57.6 55	M I	93 58	82.8	4.6	83.0		39 55	45.0	3.7	44.5	MAY		
JUN	19	71.0	3.1	70.0	76.2 70	65.2 53	I	96 58	87.7	4.5	88.0		45 66	51.1	3.5	51.0	JUN		
JUL	20	82.9	3.5	83.0	89.9 60	76.1 55	I	104 59	96.3	3.6	96.0		52 55	61.6	6.5	61.5	JUL		
AUG	20	81.0	5.3	80.5	91.7 67	73.3 64	I	107 61	96.4	4.8	96.5		52 60	61.0	7.1	58.5	AUG		
SEP	20	71.4	5.0	71.5	81.1 67	62.9 59	I	96 58	88.1	5.3	87.5		43 58	50.4	4.6	50.0	SEP		
OCT	13	56.8	4.6	55.0	65.1 52	50.1 51	M I	84 63	74.1	4.7	74.0		27 57	41.4	6.1	41.0	OCT		

RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100304 FERN RS							1951-1970										
10-DAY AND MONTHLY PERIOD MEANS							10-DAY AND MONTHLY EXTREME DAILY VALUES										
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG. YR	LOWEST AVG. YR	I	HIGH. YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW. YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS	
MAY 1	14	49.0	10.5	51.5	65.2 60	33.4 66	I	93 63	81.9	13.0	86.5	10 70	25.1	9.2	26.0	MAY 1	
MAY 11	16	44.2	12.6	41.0	68.9 57	28.0 64	I	100 68	75.4	19.5	76.0	16 53	24.1	6.7	22.5	MAY 11	
MAY 21	17	44.9	9.6	45.0	64.3 54	30.4 63	I	100 69	85.5	12.3	87.0	15 66	24.6	7.4	23.0	MAY 21	
JUN 1	19	47.0	11.8	51.0	69.1 53	24.2 65	I	100 66	76.2	21.0	86.0	18 70	25.8	6.9	25.0	JUN 1	
JUN 11	19	43.7	8.5	44.0	54.8 65	27.6 69	I	100 65	77.3	16.7	78.0	17 66	25.2	5.4	25.0	JUN 11	
JUN 21	20	41.6	12.2	38.5	68.1 69	24.3 61	I	100 69	66.3	21.1	64.5	15 70	24.1	6.8	23.0	JUN 21	
JUL 1	20	35.8	8.9	35.5	53.3 55	18.7 68	I	94 54	67.3	21.5	72.0	13 68	20.2	5.1	18.5	JUL 1	
JUL 11	20	28.8	6.7	26.5	41.1 57	18.7 60	I	69 55	45.1	13.3	43.5	12 65	17.1	4.3	17.0	JUL 11	
JUL 21	20	25.2	8.1	20.5	45.7 55	16.7 66	I	94 65	45.7	22.8	36.0	10 59	14.6	3.7	14.0	JUL 21	
AUG 1	20	28.2	9.1	23.5	47.0 62	19.2 51	I	84 60	49.1	18.0	44.0	9 67	16.6	5.7	16.0	AUG 1	
AUG 11	20	27.8	11.4	24.0	55.3 54	11.1 67	I	93 64	46.2	25.0	37.0	5 67	15.3	4.7	14.5	AUG 11	
AUG 21	20	35.8	13.2	34.0	62.3 54	17.5 70	I	94 65	64.7	23.2	67.0	8 70	18.3	10.0	16.0	AUG 21	
SEP 1	20	33.5	10.0	32.5	52.3 54	20.0 66	I	93 64	59.2	23.2	58.5	9 69	19.4	7.9	18.0	SEP 1	
SEP 11	20	40.3	11.2	37.5	65.0 54	25.4 61	I	100 69	74.8	22.1	76.0	12 69	22.5	7.3	20.5	SEP 11	
SEP 21	20	43.2	10.9	41.5	66.5 59	23.7 67	I	94 51	77.2	13.6	81.5	11 67	24.6	7.5	23.5	SEP 21	
OCT 1	18	50.4	11.9	48.0	70.2 57	26.8 52	I	100 59	84.8	16.6	93.0	14 58	28.3	10.3	26.5	OCT 1	
OCT 11	16	55.1	14.0	53.5	81.2 51	32.8 52	I	100 51	79.6	15.6	84.5	20 52	37.6	11.9	35.5	OCT 11	
OCT 21	13	65.6	8.6	66.0	75.6 57	44.6 65	I	100 66	87.6	13.8	92.0	38 65	45.9	8.4	42.0	OCT 21	
MONTH							I										
MAY	16	46.3	8.3	43.0	61.5 60	34.4 66	I	100 69	92.7	6.2	93.0	10 70	20.1	6.6	18.5	MAY	
JUN	19	44.4	5.8	43.0	60.0 53	35.7 62	I	100 69	91.2	10.5	94.0	15 70	21.2	5.6	20.0	JUN	
JUL	20	29.8	6.2	28.0	46.0 55	21.4 60	I	94 65	74.6	17.8	78.5	10 59	13.9	3.1	13.0	JUL	
AUG	20	30.8	9.1	29.5	50.4 54	16.4 67	I	94 65	72.8	20.4	81.0	5 67	12.8	4.9	12.0	AUG	
SEP	20	39.0	7.8	36.0	57.0 54	27.0 67	I	100 69	90.1	7.9	93.0	9 69	18.1	6.1	17.5	SEP	
OCT	13	58.0	10.1	57.0	74.3 51	38.6 52	I	100 66	94.6	6.9	94.0	14 58	29.3	9.5	27.0	OCT	

(con.)

Table 11 (Con.)

DRY BULB TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100304 FERNAN RS 10-DAY AND MONTHLY PERIOD MEANS										1974-1984 10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR	I	I	I	HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS	
MAY 1	8	57.5	4.2	56.5	66.3 76	53.1 64	I	I	I	76 76	68.3	4.6	68.5	40 75	44.6	3.8	45.0	MAY 1	
MAY 11	8	60.3	5.4	60.0	67.7 76	50.3 74	I	I	I	80 76	72.5	7.0	73.5	43 74	48.6	4.1	48.0	MAY 11	
MAY 21	8	64.9	7.3	62.5	82.3 83	59.2 78	I	I	I	94 83	78.1	7.9	76.5	45 75	53.4	9.4	50.5	MAY 21	
JUN 1	11	66.4	5.3	65.0	76.0 78	58.0 84	I	I	I	86 78	79.6	5.1	80.0	45 84	53.5	4.6	52.0	JUN 1	
JUN 11	11	69.9	8.2	68.0	85.6 74	57.3 81	I	I	I	92 74	80.8	7.8	81.0	51 81	57.6	6.5	56.0	JUN 11	
JUN 21	11	71.7	5.0	70.0	78.2 74	63.6 75	I	I	I	88 76	83.4	4.5	86.0	51 75	58.9	5.9	58.0	JUN 21	
JUL 1	11	72.9	6.5	71.0	91.0 75	66.4 82	I	I	I	99 75	84.9	5.5	84.0	50 79	60.8	8.9	60.0	JUL 1	
JUL 11	11	75.7	4.1	75.0	82.6 79	69.5 83	I	I	I	95 79	87.4	4.2	88.0	48 82	60.5	6.7	61.0	JUL 11	
JUL 21	10	83.2	3.0	84.0	86.9 74	78.0 81	I	I	I	97 84	92.1	3.5	92.0	59 75	72.1	6.7	70.5	JUL 21	
AUG 1	10	91.5	4.8	80.5	88.2 78	74.6 76	I	I	I	96 81	90.3	4.1	92.0	63 76	71.5	6.6	70.0	AUG 1	
AUG 11	11	78.0	7.9	78.0	91.8 77	63.0 78	I	I	I	96 81	88.5	5.3	86.0	53 78	64.6	9.3	63.0	AUG 11	
AUG 21	11	74.4	5.7	75.0	82.9 74	65.0 75	I	I	I	91 81	85.0	4.4	86.0	55 80	61.4	5.7	60.0	AUG 21	
SEP 1	11	71.6	3.4	71.0	75.7 81	64.6 83	I	I	I	88 82	81.5	4.6	81.0	52 83	59.1	4.8	59.0	SEP 1	
SEP 11	11	70.3	6.0	70.0	80.5 81	59.9 78	I	I	I	90 81	79.9	6.7	80.0	47 83	57.5	7.4	58.0	SEP 11	
SEP 21	11	65.4	7.4	66.0	74.9 76	53.6 77	I	I	I	81 74	73.3	7.3	76.0	46 84	56.8	7.3	56.0	SEP 21	
OCT 1	9	61.7	7.4	59.0	72.2 80	51.9 81	I	I	I	80 80	71.0	7.2	74.0	46 81	54.0	6.8	52.0	OCT 1	
OCT 11	9	55.4	4.3	55.0	62.1 78	47.0 84	M	I	I	72 79	63.7	5.8	62.0	41 84	47.1	4.6	48.0	OCT 11	
OCT 21	6	51.3	3.7	52.0	55.7 83	44.7 75	M	I	I	67 83	60.7	6.2	63.0	39 75	43.0	2.7	43.0	OCT 21	
MONTH										MONTH									
MAY	9	61.0	3.5	59.5	66.8 83	57.5 74	I	I	I	94 83	79.5	6.8	78.5	40 75	43.5	2.4	44.0	MAY	
JUN	11	69.3	4.7	66.0	76.2 74	62.9 81	I	I	I	92 74	86.3	3.3	86.0	45 84	51.5	3.3	51.0	JUN	
JUL	10	77.8	2.3	77.0	81.5 75	74.0 81	I	I	I	99 75	93.4	3.7	94.0	48 82	57.9	6.1	58.5	JUL	
AUG	10	77.8	4.3	78.5	84.4 81	72.2 75	I	I	I	96 81	91.1	4.0	92.0	53 78	58.8	4.4	58.5	AUG	
SEP	11	69.2	3.8	68.0	74.1 76	63.4 77	I	I	I	90 81	82.6	5.1	81.0	46 84	52.6	5.4	53.0	SEP	
OCT	6	54.8	2.6	53.5	59.1 78	52.5 82	I	I	I	80 80	68.7	4.8	67.5	39 75	42.8	2.4	43.0	OCT	

RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100304 FERNAN RS										1974-1984									
10-DAY AND MONTHLY PERIOD MEANS										10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR	I	I	I	HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS	
MAY 1	8	49.6	7.5	49.0	61.1 83	39.1 74	I	I	I	100 83	88.9	13.9	93.5	18 74	26.9	7.6	24.5	MAY 1	
MAY 11	8	53.5	13.3	55.0	70.1 84	32.5 76	I	I	I	100 78	82.5	12.2	82.5	15 76	25.1	8.0	26.0	MAY 11	
MAY 21	8	45.1	7.6	47.5	53.1 81	31.1 83	I	I	I	100 76	72.1	18.1	73.5	16 76	26.5	9.8	23.5	MAY 21	
JUN 1	11	48.4	10.4	50.0	69.5 84	33.7 79	I	I	I	100 83	78.0	20.6	84.0	16 78	28.3	9.4	25.0	JUN 1	
JUN 11	11	48.4	10.7	51.0	68.1 83	29.5 74	I	I	I	100 83	75.3	16.1	71.0	15 74	28.2	9.2	31.0	JUN 11	
JUN 21	11	47.7	10.7	53.0	59.4 83	31.2 77	I	I	I	89 83	70.9	14.8	73.0	16 77	28.8	8.0	31.0	JUN 21	
JUL 1	11	47.2	9.3	48.0	61.0 78	31.7 77	I	I	I	94 83	72.8	18.4	78.0	17 77	29.4	8.6	27.0	JUL 1	
JUL 11	11	43.8	10.8	45.0	62.0 83	30.6 79	I	I	I	100 82	74.4	21.8	88.0	18 79	26.8	7.2	24.0	JUL 11	
JUL 21	10	33.6	5.9	32.0	43.1 75	25.5 74	I	I	I	86 77	55.4	17.2	54.0	14 80	21.3	4.9	21.0	JUL 21	
AUG 1	10	35.1	9.8	33.5	50.6 76	23.1 78	I	I	I	90 74	53.8	18.3	50.5	15 77	22.4	6.3	22.0	AUG 1	
AUG 11	11	40.5	12.5	38.0	68.2 78	19.9 77	I	I	I	100 78	67.9	25.6	63.0	15 77	25.4	6.8	25.0	AUG 11	
AUG 21	11	45.7	9.2	45.0	58.5 75	29.4 74	I	I	I	100 80	80.9	17.3	85.0	19 84	27.7	6.5	26.0	AUG 21	
SEP 1	11	45.2	9.7	43.0	62.5 83	30.0 76	I	I	I	100 79	71.5	18.7	71.0	11 82	28.8	9.8	30.0	SEP 1	
SEP 11	11	43.3	3.9	41.0	59.9 83	29.8 79	I	I	I	93 83	66.8	17.0	63.0	16 76	28.7	8.3	27.0	SEP 11	
SEP 21	11	47.8	12.0	51.0	65.8 82	27.6 74	I	I	I	93 84	68.1	21.7	72.0	22 77	33.4	7.6	32.0	SEP 21	
OCT 1	9	49.3	12.4	51.0	63.9 75	26.4 79	I	I	I	94 81	70.6	21.6	75.0	17 79	34.1	8.6	37.0	OCT 1	
OCT 11	9	56.9	3.9	60.0	67.4 82	40.1 78	I	I	I	100 83	81.1	15.5	85.0	16 78	39.3	12.1	46.0	OCT 11	
OCT 21	6	60.9	13.0	63.0	78.3 75	45.5 81	I	I	I	100 83	80.7	18.2	82.0	24 75	37.0	8.7	36.0	OCT 21	
MONTH										MONTH									
MAY	8	49.2	6.5	46.5	58.7 81	42.7 76	I	I	I	100 83	93.9	7.0	96.5	15 76	21.9	5.8	21.0	MAY	
JUN	11	48.2	8.9	47.0	60.2 83	34.5 74	I	I	I	100 83	87.1	12.2	87.0	15 74	23.2	7.7	23.0	JUN	
JUL	10	40.4	4.8	40.0	45.8 81	33.4 79	I	I	I	100 82	85.6	11.5	88.5	14 80	20.0	4.1	20.5	JUL	
AUG	10	40.0	5.7	39.0	48.2 76	33.3 77	I	I	I	100 80	88.9	13.6	92.5	15 77	19.9	4.3	18.5	AUG	
SEP	11	45.4	7.7	43.0	56.0 83	32.6 74	I	I	I	100 79	84.4	11.1	87.0	11 82	24.3	8.6	22.0	SEP	
OCT	6	57.4	8.7	57.0	67.7 75	44.6 78	I	I	I	100 83	87.8	13.3	91.0	16 78	31.8	9.8	36.0	OCT	

(con.)

Table 11 (Con.)

DRY BULB TEMPERATURE

STATION NUMBER 100409 KINGSTON RS 10-DAY AND MONTHLY PERIOD MEANS								MEAN, STANDARD DEVIATION, AND EXTREME VALUES 1951-1970 10-DAY AND MONTHLY EXTREME DAILY VALUES										PRD. BEGINS	
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR		HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW			PRD. BEGINS	
MAY 1	9	59.0	7.8	57.0	74.1 66	50.5 61	I	90 66	72.0	9.5	72.0	39 61	44.8	3.7	45.0			MAY 1	
MAY 11	10	64.9	3.0	64.5	69.1 63	59.0 66	I	84 70	77.7	3.7	77.0	39 67	49.4	6.7	47.5			MAY 11	
MAY 21	11	67.1	3.9	67.0	74.9 63	59.9 68	I	87 56	80.9	3.8	83.0	45 64	53.7	4.6	54.0			MAY 21	
JUN 1	20	69.3	5.8	67.5	79.3 69	60.2 54	I	93 70	82.2	5.2	82.0	45 54	56.1	7.3	54.0			JUN 1	
JUN 11	20	71.1	5.9	69.0	83.3 61	63.6 54	I	96 61	84.0	5.5	83.0	50 56	57.9	5.1	57.0			JUN 11	
JUN 21	20	71.0	5.1	69.5	78.8 62	60.8 69	I	95 55	82.9	6.1	82.0	49 53	56.9	5.3	58.0			JUN 21	
JUL 1	20	77.4	5.7	76.5	89.4 68	65.6 55	I	95 70	89.6	4.2	90.0	53 66	63.3	7.6	60.5			JUL 1	
JUL 11	20	82.1	5.0	82.5	92.9 60	74.3 57	I	101 67	92.6	5.0	93.5	61 63	70.9	5.9	70.0			JUL 11	
JUL 21	20	83.2	4.8	84.0	89.8 51	73.7 70	I	100 59	92.0	4.0	93.0	54 54	70.9	8.8	71.5			JUL 21	
AUG 1	20	81.9	5.0	83.0	89.9 61	71.8 62	I	106 61	91.6	5.7	93.0	57 62	68.9	7.5	70.0			AUG 1	
AUG 11	20	81.2	6.7	81.5	95.4 67	65.6 68	I	99 67	91.4	4.7	91.5	52 64	69.9	10.1	72.0			AUG 11	
AUG 21	20	75.2	7.2	74.5	87.7 70	61.4 60	I	98 67	88.2	7.8	89.0	50 60	62.2	8.7	60.0			AUG 21	
SEP 1	20	74.5	6.8	73.5	87.0 55	63.0 70	I	93 58	85.2	5.6	85.0	48 61	60.9	9.2	60.0			SEP 1	
SEP 11	20	69.3	6.7	70.0	80.6 53 M	55.8 65	I	95 53	82.3	7.5	84.5	44 65	53.7	5.7	55.0			SEP 11	
SEP 21	20	67.3	8.3	64.5	80.8 52	53.6 59	I	92 67	79.1	9.4	77.5	45 61	53.2	7.2	51.5			SEP 21	
OCT 1	10	63.3	6.2	63.0	75.8 52	53.2 69	I	82 70	75.9	6.0	76.5	43 70	51.9	8.0	52.0			OCT 1	
OCT 11	7	57.2	5.7	57.0	67.8 63	51.0 66	I	75 64	66.6	7.5	68.0	44 69	47.7	4.8	47.0			OCT 11	
OCT 21	7	52.7	5.4	51.0	62.9 65	47.2 67	I	70 69	64.3	4.8	64.0	37 64	42.6	5.5	41.0			OCT 21	
MONTH																		MONTH	
MAY	9	63.9	2.7	62.0	68.1 69	61.0 64	I	90 66	83.0	3.5	83.0	39 67	43.3	3.0	44.0			MAY	
JUN	20	70.5	3.3	69.5	78.5 61	65.1 53	I	96 61	86.9	4.6	87.0	45 54	52.1	3.8	52.0			JUN	
JUL	20	81.0	3.0	81.0	88.2 60	76.3 55	I	101 67	94.8	3.4	94.5	53 66	60.6	5.9	59.0			JUL	
AUG	20	79.3	4.8	79.0	88.8 67	71.7 64	I	106 61	94.9	3.8	95.5	50 60	60.1	7.2	58.5			AUG	
SEP	20	70.4	5.4	69.5	78.7 63	62.0 59	I	95 53	87.6	4.9	88.5	44 65	49.8	4.3	48.5			SEP	
OCT	7	57.2	3.4	56.0	61.7 65	52.2 69	I	82 70	76.4	4.5	75.0	37 64	41.1	2.5	41.0			OCT	

RELATIVE HUMIDITY

STATION NUMBER 100409 KINGSTON RS 10-DAY AND MONTHLY PERIOD MEANS								MEAN, STANDARD DEVIATION, AND EXTREME VALUES 1951-1970 10-DAY AND MONTHLY EXTREME DAILY VALUES										PRD. BEGINS	
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR		HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW			PRD. BEGINS	
MAY 1	9	45.5	13.8	40.0	69.7 61	31.0 66	I	86 63	72.3	14.5	76.0	15 66	26.7	12.6	21.0			MAY 1	
MAY 11	10	39.4	7.8	37.5	56.6 52 M	29.9 64	I	91 67	72.1	18.0	77.5	15 64	21.5	5.3	20.0			MAY 11	
MAY 21	11	41.9	7.3	40.0	59.0 68	32.3 64	I	94 69	80.7	12.6	88.0	13 63	20.5	4.2	22.0			MAY 21	
JUN 1	20	46.2	9.8	48.5	62.1 59	29.1 65	I	88 67	72.9	17.4	81.0	14 55	25.4	7.8	25.0			JUN 1	
JUN 11	20	43.4	8.4	43.5	57.4 65	25.8 69	I	94 70	73.0	15.2	72.0	13 61	24.6	5.7	24.5			JUN 11	
JUN 21	20	43.0	9.8	42.0	63.0 69	26.7 62	I	94 69	71.8	17.6	78.5	16 70	24.6	5.8	25.0			JUN 21	
JUL 1	20	37.1	8.9	35.0	57.4 55	21.5 68	I	94 66	64.7	20.1	63.0	15 68	21.3	4.6	20.5			JUL 1	
JUL 11	20	30.6	6.5	29.5	43.5 57	18.9 60	I	75 57	48.4	14.4	46.0	12 60	19.2	3.5	19.5			JUL 11	
JUL 21	20	26.8	7.4	23.0	42.4 55	19.6 60	I	89 64	45.6	21.8	34.0	11 52	16.4	3.1	16.0			JUL 21	
AUG 1	20	29.7	8.9	25.5	52.4 62	20.0 59	I	94 60	54.3	20.0	54.0	11 61	17.1	4.6	16.5			AUG 1	
AUG 11	20	28.9	10.7	25.0	58.0 68	13.6 67	I	93 68	50.1	24.2	41.0	11 67	15.4	3.8	15.0			AUG 11	
AUG 21	20	36.1	13.5	33.0	58.3 65	17.3 70	I	89 54	62.1	23.9	71.0	10 66	18.7	6.8	17.5			AUG 21	
SEP 1	20	34.1	10.0	31.5	53.2 70	20.6 55	I	100 70	62.4	24.4	59.0	11 67	19.2	5.8	18.5			SEP 1	
SEP 11	20	41.8	12.5	41.5	64.4 59	22.1 53 M	I	94 65	77.4	19.7	88.0	11 53	21.4	6.5	19.5			SEP 11	
SEP 21	20	43.1	12.3	43.5	71.9 59	23.0 52	I	94 51	77.2	18.3	84.5	8 67	23.6	9.4	21.5			SEP 21	
OCT 1	10	45.2	10.5	44.0	62.1 69	24.3 52	I	93 69	75.5	18.2	77.0	16 52	23.7	5.3	23.0			OCT 1	
OCT 11	7	49.2	10.5	45.0	63.0 65	35.1 69	I	100 67	80.0	19.1	86.0	23 69	30.4	5.0	31.0			OCT 11	
OCT 21	7	60.6	7.4	62.0	67.3 67	45.6 65	I	100 67	89.7	9.1	92.0	27 70	34.4	3.6	35.0			OCT 21	
MONTH																		MONTH	
MAY	9	41.6	4.5	40.0	50.5 61	37.2 65	I	94 69	87.4	5.6	88.0	13 63	16.4	1.9	17.0			MAY	
JUN	20	44.2	5.0	43.0	52.1 53	34.2 61	I	94 70	86.6	5.3	87.5	13 61	20.8	5.0	19.5			JUN	
JUL	20	31.3	5.5	29.0	45.0 55	21.2 60	I	94 66	72.6	16.8	76.5	11 52	15.9	2.7	16.0			JUL	
AUG	20	31.7	8.4	29.5	43.9 64	17.9 67	I	94 60	71.9	19.2	74.5	9 61	13.6	3.1	13.0			AUG	
SEP	20	39.7	8.6	38.5	61.6 59	26.6 57	I	100 70	88.3	10.8	93.0	8 67	17.0	5.1	16.0			SEP	
OCT	7	53.2	4.6	53.0	60.5 67	46.5 66	I	100 67	93.9	4.7	93.0	16 52	24.9	5.3	24.0			OCT	

(con.)

Table 11 (Con.)

DRY BULB TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100412 MAGEE RS 10-DAY AND MONTHLY PERIOD MEANS										1963-1972 10-DAY AND MONTHLY EXTREME DAILY VALUES										
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR				HIGH.YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH		LOW.YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS	
JUN 1	8	67.7	7.0	67.5	76.0 69	58.0 71				91 70	79.8	8.6	80.5		44 66	56.0	9.0	52.5	JUN 1	
JUN 11	9	66.3	5.2	64.0	76.1 69	61.5 65				87 70	80.1	5.3	80.0		46 72	52.9	3.3	53.0	JUN 11	
JUN 21	9	67.5	5.5	66.0	75.8 70	57.5 69				89 70	81.1	5.0	80.0		44 71	51.6	4.6	52.0	JUN 21	
JUL 1	9	76.0	6.8	76.0	88.0 68	65.5 71				95 64	87.1	5.6	87.0		46 71	60.8	9.4	58.0	JUL 1	
JUL 11	10	76.9	5.0	77.5	83.3 67	67.9 72				100 67	89.4	6.0	90.0		50 72	63.4	6.8	63.5	JUL 11	
JUL 21	10	78.9	4.7	79.5	85.5 71	69.8 70				93 68	88.2	3.8	88.5		56 65	65.3	7.6	62.5	JUL 21	
AUG 1	10	81.4	4.6	82.0	88.5 71	71.1 64				95 71	90.3	4.1	91.0		54 64	66.4	7.4	67.5	AUG 1	
AUG 11	10	77.7	7.8	77.5	92.9 67	63.7 68				97 67	88.6	4.7	87.0		51 68	65.2	11.0	64.0	AUG 11	
AUG 21	10	74.7	7.6	75.5	84.5 70	63.5 65				96 69	88.3	7.0	90.0		52 65	61.5	8.8	60.0	AUG 21	
SEP 1	10	71.1	8.0	71.0	82.2 63	62.2 64				91 69	82.3	7.0	83.5		47 70	58.2	10.1	55.0	SEP 1	
SEP 11	10	63.1	6.4	63.0	73.1 67	53.3 65				86 63	74.9	8.0	76.5		39 65	49.7	6.4	50.5	SEP 11	
SEP 21	7	66.8	8.7	64.0	78.6 63	55.7 71				88 66	81.1	6.1	80.0		40 72	50.6	6.0	50.0	SEP 21	
MONTH																				MONTH
JUN	8	66.6	3.0	66.0	71.4 70	62.5 71				91 70	85.0	3.6	84.5		44 71	48.6	3.5	50.0	JUN	
JUL	9	77.6	2.4	77.0	81.2 67	73.1 72				100 67	92.2	3.8	92.0		46 71	55.7	5.4	57.0	JUL	
AUG	10	77.8	5.4	78.5	86.3 67	68.5 64				97 67	92.7	3.7	93.5		51 68	56.9	5.0	55.5	AUG	
SEP	7	68.0	7.3	67.0	76.7 67	60.3 71				91 69	84.9	5.9	88.0		39 65	48.4	4.8	47.0	SEP	

RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100412 MAGEE RS 10-DAY AND MONTHLY PERIOD MEANS										1963-1972 10-DAY AND MONTHLY EXTREME DAILY VALUES											
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG,YR	LOWEST AVG,YR			HIGH,YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH		LOW,YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS			
JUN 1	8	50.0	10.3	50.5	64.4 71	31.6 65			100 66	78.6	18.9	84.5		19 72	24.6	5.2	23.0	JUN 1			
JUN 11	9	51.0	8.9	50.0	62.5 70	37.7 67			94 70	82.3	9.4	83.0		21 67	30.1	5.9	31.0	JUN 11			
JUN 21	9	48.8	11.9	46.0	77.0 69	35.3 64			100 69	84.3	13.5	86.0		18 64	24.0	3.4	24.0	JUN 21			
JUL 1	9	36.8	8.5	36.0	51.0 69	23.5 68			88 67	67.1	18.8	72.0		15 68	22.7	4.7	22.0	JUL 1			
JUL 11	10	35.9	7.9	34.5	48.0 72	24.7 67			89 63	61.5	18.2	65.0		15 67	21.1	4.4	20.0	JUL 11			
JUL 21	10	32.5	8.9	29.5	47.6 70	22.9 66			89 72	58.4	25.0	51.0		15 71	18.7	3.3	18.5	JUL 21			
AUG 1	10	31.2	8.7	28.5	49.8 64	22.1 66			88 70	54.6	17.4	49.0		11 67	17.6	6.5	15.5	AUG 1			
AUG 11	10	34.1	14.3	31.0	61.0 68	14.6 67			100 68	61.3	27.5	65.5		9 67	18.1	5.9	17.5	AUG 11			
AUG 21	10	39.3	15.0	39.0	61.3 65	19.6 67			100 71	69.9	27.3	76.5		8 66	20.7	8.7	20.0	AUG 21			
SEP 1	10	40.6	12.3	38.5	58.5 71	26.0 66			100 71	67.3	23.1	74.5		13 69	23.0	6.9	23.0	SEP 1			
SEP 11	10	48.3	11.4	45.5	70.6 68	30.3 71			100 68	81.6	20.3	90.0		15 69	27.4	8.0	26.5	SEP 11			
SEP 21	7	45.1	13.2	42.0	61.8 69	26.1 67			100 71	88.1	11.5	93.0		10 67	22.3	6.9	22.0	SEP 21			
MONTH																		MONTH			
JUN	8	50.6	2.9	50.0	53.9 72	45.4 65			100 69	92.4	6.7	93.0		18 64	21.3	2.2	21.5	JUN			
JUL	10	35.1	4.2	35.5	39.8 63	27.8 67			89 72	83.6	5.6	84.0		15 71	17.2	2.3	17.0	JUL			
AUG	10	35.0	11.1	31.5	52.9 64	19.5 67			100 71	79.3	22.8	88.5		8 66	15.2	6.4	15.0	AUG			
SEP	7	43.1	8.4	47.0	53.5 64	29.9 67			100 71	92.0	7.7	93.0		10 67	18.0	6.0	18.0	SEP			

(con.)

Table 11 (Con.)

DRY BULB TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100306 MT COVER D ALENE LO 10-DAY AND MONTHLY PERIOD MEANS							1954-1970 10-DAY AND MONTHLY EXTREME DAILY VALUES										
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG.YR	LOWEST AVG.YR	HIGH, YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW, YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS		
JUL 1	14	70.3	4.6	69.5	80.7 68	62.1 62	I 88 68	81.8	2.9	82.0	43 66	56.3	7.7	56.5	JUL 1		
JUL 11	17	74.0	5.8	73.0	85.5 60	65.6 68	I 93 67	84.2	5.0	84.0	52 54	63.2	8.1	60.0	JUL 11		
JUL 21	17	75.1	6.2	76.0	84.7 58	65.2 54	I 92 59	84.2	6.0	85.0	46 54	63.3	10.0	64.0	JUL 21		
AUG 1	17	73.2	6.3	73.0	84.4 58	62.4 62	I 99 61	84.1	7.1	85.0	46 64	60.2	8.2	60.0	AUG 1		
AUG 11	16	73.6	7.3	72.0	88.5 67	60.5 54	I 93 61	83.6	6.5	84.0	46 60	61.4	10.7	62.5	AUG 11		
AUG 21	12	71.2	7.0	71.0	81.2 70	59.3 59	I 95 67	85.0	9.1	88.5	45 56	57.1	8.3	57.0	AUG 21		
MONTH							I										MONTH
JUL	15	73.5	4.0	73.0	80.2 60	66.6 54	I 93 67	87.0	3.8	88.0	43 66	53.5	6.0	54.0	JUL		
AUG	12	73.6	5.8	73.0	82.3 58	66.0 59	I 99 61	89.5	6.1	90.0	45 56	54.8	5.4	56.0	AUG		

RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100306 MT COVER D ALENE LO							1954-1970										
10-DAY AND MONTHLY PERIOD MEANS							10-DAY AND MONTHLY EXTREME DAILY VALUES										
PRD.	NO.		STD.		HIGHEST	LOWEST		AVG.	STD.	MEDIAN		AVG.	STD.	MEDIAN	PRD.		
BEGINS	YRS	MEAN	DEV.	MEDIAN	AVG,YR	AVG,YR	HIGH,YR	HIGH	DEV.	HIGH	LOW,YR	LOW	DEV.	LOW	BEGINS		
JUL 1	14	44.7	7.9	46.0	55.6 54	31.2 68	I 100 63	74.7	19.7	80.0	16 58	27.1	6.8	26.0	JUL 1		
JUL 11	17	39.2	8.5	38.0	51.7 68	22.8 60	I 89 70	61.1	17.3	57.0	15 60	24.5	5.5	25.0	JUL 11		
JUL 21	17	35.0	9.9	30.0	57.7 55	25.4 66	I 100 70	60.8	26.3	47.0	12 69	21.5	4.4	21.0	JUL 21		
AUG 1	17	37.3	12.7	33.0	67.9 62	24.1 61	I 100 64	64.5	21.2	55.0	11 61	21.2	6.5	18.0	AUG 1		
AUG 11	16	35.3	11.9	34.0	60.8 54	15.0 67	I 100 59	60.9	27.1	54.5	8 67	20.9	6.5	21.5	AUG 11		
AUG 21	12	37.8	12.4	36.0	57.8 56 M	21.7 70	I 94 56	66.8	25.0	76.0	11 67	18.6	6.4	17.5	AUG 21		
MONTH							I										MONTH
JUL	15	39.4	6.6	37.0	51.6 55 M	27.2 60	I 100 70	86.1	14.3	89.0	12 69	19.9	3.2	19.0	JUL		
AUG	12	34.6	8.8	31.0	51.4 62 M	21.7 67	I 100 64	76.8	18.3	80.5	8 67	15.2	4.0	16.0	AUG		

DRY BULB TEMPERATURE

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100417 SPYGLASS LO 10-DAY AND MONTHLY PERIOD MEANS							1951-1970 10-DAY AND MONTHLY EXTREME DAILY VALUES										
PRD. BEGINS	NO. YRS	MEAN	STD. DEV.	MEDIAN	HIGHEST AVG,YR	LOWEST AVG,YR	I	HIGH,YR	AVG. HIGH	STD. DEV.	MEDIAN HIGH	LOW,YR	AVG. LOW	STD. DEV.	MEDIAN LOW	PRD. BEGINS	
JUL 1	15	65,8	5,5	65,0	78,1 68	57,8 55	I	85 68	77,9	3,9	78,0	43 62	51,6	6,9	51,0	JUL 1	
JUL 11	20	69,8	5,9	68,5	83,3 60	60,1 52	I	90 60	80,4	6,3	82,0	48 63	57,9	7,1	57,0	JUL 11	
JUL 21	20	71,0	4,9	71,5	78,1 51	61,3 70	I	87 59	80,2	4,4	81,0	39 54	57,7	9,5	56,0	JUL 21	
AUG 1	20	70,1	5,7	70,5	79,3 61	58,9 62	I	95 61	80,4	5,7	80,5	43 64	56,1	8,1	56,0	AUG 1	
AUG 11	19	70,7	6,6	70,0	83,5 67	59,7 59	I	89 61	81,3	4,8	82,0	41 64	58,2	10,3	57,0	AUG 11	
AUG 21	13	66,3	7,0	64,0	76,1 61 M	54,4 59	I	89 69	80,4	7,9	85,0	39 60	52,2	8,2	50,0	AUG 21	
MONTH							I										MONTH
JUL	18	68,9	3,4	67,5	77,7 60	62,5 52	I	90 60	83,3	3,8	83,5	39 54	49,8	6,1	48,5	JUL	
AUG	13	69,6	5,3	67,0	77,4 61 M	62,0 59	I	95 61	85,4	4,6	85,0	39 60	48,8	6,2	47,0	AUG	

RELATIVE HUMIDITY

MEAN, STANDARD DEVIATION, AND EXTREME VALUES

STATION NUMBER 100417 SPYGLASS LO							1951-1970									
10-DAY AND MONTHLY PERIOD MEANS							10-DAY AND MONTHLY EXTREME DAILY VALUES									
PRD.	NO.		STD.		HIGHEST	LOWEST		AVG.		STD.	MEDIAN		AVG.	STD.	MEDIAN	PRD.
BEGINS	YRS	MEAN	DEV.	MEDIAN	AVG.YR	AVG.YR	HIGH, YR	HIGH	DEV.	HIGH	LOW, YR	LOW	LOW	DEV.	LOW	BEGINS
JUL 1	15	49.8	10.3	50.0	64.9	58	28.5	68	19.7	87.0	18	66	30.1	5.6	29.0	JUL 1
JUL 11	20	43.9	9.4	42.5	61.9	56	25.2	60	19.0	70.5	17	67	28.8	8.5	28.5	JUL 11
JUL 21	20	39.3	8.9	36.5	56.4	70	26.9	62	22.8	55.0	15	66	24.1	6.4	23.0	JUL 21
AUG 1	20	41.1	11.8	39.5	63.8	62	23.4	51	21.0	69.0	12	67	23.2	6.5	21.5	AUG 1
AUG 11	19	37.3	11.9	36.0	63.8	54	17.7	67	22.4	60.0	9	67	21.5	7.8	19.0	AUG 11
AUG 21	13	42.9	13.8	45.0	65.0	53	22.9	67	25.7	83.0	11	69	22.8	9.1	24.0	AUG 21
MONTH																MONTH
JUL	18	44.2	7.1	45.5	52.8	54	30.2	60	15.0	93.0	15	66	23.3	5.1	22.5	JUL
AUG	13	39.1	8.7	42.0	48.7	59	23.2	67	19.9	87.0	9	67	17.2	6.2	16.0	AUG

Table 12--Frequencies of afternoon dry bulb and relative humidity values. For indicated years of record and observation times noted in table 11 caption

DRY BULB TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100304		FERNAN RS		TEMPERATURE VALUES																		1951-1970					
PRD.	BELOW	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	PRD.						
BEGINS	0	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99	AND ABOVE	BEGINS						
MAY 1										29	86	243	121	179	93	114	79	36	21				MAY 1						
MAY 11									6	25	44	100	144	150	175	156	138	38	25				MAY 11						
MAY 21										11	27	96	128	155	176	139	118	91	43	16			MAY 21						
JUN 1										26	47	89	147	189	179	137	121	42	21				JUN 1						
JUN 11										11	26	100	153	121	174	153	137	100	26				JUN 11						
JUN 21											30	60	160	140	200	175	130	45	45		15		JUN 21						
JUL 1											15	35	70	65	130	150	180	180	120	55			JUL 1						
JUL 11													5	50	90	140	200	230	185	90	10		JUL 11						
JUL 21													9	18	23	68	100	182	241	255	100	5	JUL 21						
AUG 1													5	45	15	90	130	200	240	200	60	15	AUG 1						
AUG 11												5	20	45	30	70	120	225	220	150	80	35	AUG 11						
AUG 21												23	59	64	127	168	164	145	100	55	77	18	AUG 21						
SEP 1												25	45	60	100	200	175	170	130	80	15		SEP 1						
SEP 11										5	15	40	115	140	175	100	160	150	90	10			SEP 11						
SEP 21										10	20	70	151	141	196	131	126	80	65	10			SEP 21						
OCT 1										28	89	162	140	123	162	162	106	28					OCT 1						
OCT 11										38	138	238	256	175	100	38	19						OCT 11						
OCT 21							7	7	35	147	168	273	168	105	56	35							OCT 21						
MONTH																													
MAY									2	21	49	140	131	160	152	138	113	57	31	6			MAY						
JUN										12	34	83	153	150	184	155	129	62	31		5		JUN						
JUL											5	15	31	45	95	129	187	218	189	82			JUL						
AUG												10	29	52	60	111	139	189	184	132	73	23	AUG						
SEP										5	12	45	104	114	157	144	154	134	95	33	5		SEP						
OCT							2	2	10	66	129	220	187	135	110	83	46	10					OCT						

RELATIVE HUMIDITY

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100304		FERNAN RS																		HUMIDITY VALUES										1951-1970											
PRD. BEGINS		0 TO 4	5 TO 9	10 TO 14	15 TO 19	20 TO 24	25 TO 29	30 TO 34	35 TO 39	40 TO 44	45 TO 49	50 TO 54	55 TO 59	60 TO 64	65 TO 69	70 TO 74	75 TO 79	80 TO 84	85 TO 89	90 TO 94	95 TO 99	100	PRD. BEGINS																				
MAY 1				14	43	57	79	86	57	157	107	79	29	64	36	21	29	57	50	36			MAY 11																				
MAY 11					56	100	125	131	94	81	106	56	75	25	13	25	25	13	6	44		25	MAY 11																				
MAY 21					43	70	144	107	150	96	64	59	70	21	16	21	27	43	43	11		16	MAY 21																				
JUN 1					26	84	105	111	95	137	84	63	63	32	26	32	37	42	21	26	5	11	JUN 1																				
JUN 11					21	68	205	105	142	74	84	79	32	42	16	42	16	5	37	21		11	JUN 11																				
JUN 21					55	95	160	150	100	105	50	60	65	40	40	15	10	15	10	10		20	JUN 21																				
JUL 1				15	110	140	170	180	135	50	35	20	30	15	25	20	15	10	15	15			JUL 1																				
JUL 11				45	185	180	170	165	100	70	45		25	5	10								JUL 11																				
JUL 21				114	305	191	155	91	55	27	5	9	5	23			14	5		5			JUL 21																				
AUG 1		10	70	235	185	150	120	80	30	35	20	15	20		5	15	5	5					AUG 1																				
AUG 11		15	110	200	235	145	75	80	50	10	5	15		10	15	5	10	15	5				AUG 11																				
AUG 21		32	73	132	127	132	105	73	55	50	55	18	27	18	27	27	18	23	9				AUG 21																				
SEP 1		5	45	105	180	210	110	90	55	45	50	25	15	5	20	5	5	20	10				SEP 1																				
SEP 11			5	50	150	205	125	90	70	75	50	20	25	15	30	10	5	20	25		30		SEP 11																				
SEP 21			15	35	95	136	126	126	70	75	80	50	35	40	10	30	40	15	20				SEP 21																				
OCT 1			6	28	73	106	101	89	67	89	73	67	61	28	28	28	22	56	50		28		OCT 1																				
OCT 11					31	38	94	94	113	81	94	69	81	69	44	44	25	63	56		6		OCT 11																				
OCT 21								35	98	84	56	112	119	119	84	49	63	70	77		35		OCT 21																				
MONTH																						MONTH																					
MAY			4	47	76	119	109	105	109	90	64	60	35	21	23	27	37	33	29		14		MAY																				
JUN				34	83	157	122	112	105	72	67	53	38	28	29	21	21	22	19	2	14		JUN																				
JUL			60	203	171	165	144	95	48	27	10	19	15	11	8	10	5	5	6				JUL																				
AUG		19	84	187	181	142	100	77	45	32	27	16	16	11	19	13	11	13	5				AUG																				
SEP		2	22	63	142	184	120	102	65	65	60	32	25	20	20	15	17	18	18		10		SEP																				
OCT			2	10	37	52	68	75	91	85	75	81	85	68	50	39	35	62	60		23		OCT																				

(con.)

Table 12 (Con.)

DRY BULB TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100304																		FERNAN RS										1974-1984										PRD. BEGINS	PRD. ENDS
		TEMPERATURE VALUES																																							
PRD.	BELOW	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100																			
BEGINS	0	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99	ABOVE																			
MAY 1										38	125	213	225	238	63	50	50														MAY 1										
MAY 11										13	138	138	163	200	175	113	50	13													MAY 11										
MAY 21											34	114	239	182	125	91	125	57	11	23											MAY 21										
JUN 1											9	92	183	183	147	156	138	73	18												JUN 1										
JUN 11												100	64	145	200	173	118	55	109	36											JUN 11										
JUN 21												29	95	124	114	210	200	143	86												JUN 21										
JUL 1												27	45	155	127	209	191	118	73	27	27										JUL 1										
JUL 11										9			36	91	100	200	182	191	127	55	9										JUL 11										
JUL 21													17	9	17	95	155	250	302	129	26										JUL 21										
AUG 1														10	67	67	269	192	202	183	10										AUG 1										
AUG 11												9	64	45	109	173	109	173	155	127	36										AUG 11										
AUG 21													74	132	124	66	248	215	132	8											AUG 21										
SEP 1													18	55	91	227	218	255	100	36											SEP 1										
SEP 11											19	19	130	120	139	204	194	120	46	9											SEP 11										
SEP 21											38	67	192	125	183	212	154	29													SEP 21										
OCT 1												101	146	191	169	169	157	56	11												OCT 1										
OCT 11										73	98	207	366	171	37	49															OCT 11										
OCT 21									14	164	274	260	164	110	14																OCT 21										
MONTH																														MONTH											
MAY										16	97	153	210	206	121	85	77	24	4	8											MAY										
JUN											3	74	114	151	154	179	151	90	71	12											JUN										
JUL											3	9	33	83	80	167	176	188	170	71	21										JUL										
AUG												3	48	66	101	101	209	194	161	101	15										AUG										
SEP											19	34	124	112	183	211	202	84	28	3											SEP										
OCT									4	74	152	201	242	152	78	74	20	4													OCT										

RELATIVE HUMIDITY

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		FERNAN RS																		1974-1984										PRD. BEGINS	PRD. ENDS		
		HUMIDITY VALUES																															
PRD.	BEGINS	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100											
		10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	100										
		4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99												
MAY	1				13	50	50	125	113	75	88	200	75	63	25	13	25		38				50								MAY	1	
MAY	11				25	63	50	138	63	50	88	50	63	75	50	88	50	50	50	25			25								MAY	11	
MAY	21				11	45	136	148	57	125	125	102	114	11	34	45		23	11				11								MAY	21	
JUN	1				9	55	92	73	174	101	55	128	101	64	37	9	18	18	9	18			37								JUN	1	
JUN	11				27	45	73	109	109	82	109	136	82	45	82	18		36		18			18								JUN	11	
JUN	21				19	29	114	124	152	38	57	105	114	114	38	29	19	29	19												JUN	21	
JUL	1				9	36	73	118	127	145	118	118	73	27	9	64	36	9	9	27											JUL	1	
JUL	11				9	82	155	109	109	155	109	73	82	27				18	18	45			9								JUL	11	
JUL	21				9	26	181	190	198	164	78	52	26	17		17	9														JUL	21	
AUG	1				58	163	212	173	67	135	38	29	38	29	48					10											AUG	1	
AUG	11				73	82	173	164	118	91	64	64	55	18		27	18			18											AUG	11	
AUG	21				8	74	107	116	174	116	74	50	74	50	41	33	8	8	41		8										AUG	21	
SEP	1				9	9	55	73	145	118	145	109	82	82	45	18	36	27	18	9	9		9								SEP	1	
SEP	11				9	19	148	241	83	56	130	111	65	56	19	28		19	9	9											SEP	11	
SEP	21					38	87	77	163	154	96	106	67	48	67	19	19	10	29	19											SEP	21	
OCT	1				22	11	67	67	124	180	169	67	56	45	34	45	34	11	45	22											OCT	1	
OCT	11				24	12	12	24	37	85	207	122	61	122	61	98	61		12	49											OCT	11	
OCT	21					14			68	164	82	82	110	68	55	55	123	27	55	27											OCT	21	
MONTH																														MONTH			
MAY					16	52	81	137	77	85	101	117	85	48	36	48	24	24	32	8											MAY		
JUN					19	43	93	102	145	74	74	123	99	74	52	19	12	28	9	12											JUN		
JUL				3	15	101	140	143	134	125	92	71	60	24	3	27	15	9	12	24											JUL		
AUG					45	104	161	149	122	113	60	48	57	33	30	21	9	3	15	9											AUG		
SEP				3	6	37	102	155	121	118	112	99	71	50	34	28	16	16	16	12											SEP		
OCT					16	12	29	33	78	143	156	90	74	78	49	66	70	12	37	33											OCT		

(con.)

Table 12 (Con.)

DRY BULB TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100409		KINGSTON RS		TEMPERATURE VALUES																		1951-1970					
PRD. BEGINS	BELOW 0	0 TO 4	5 TO 9	10 TO 14	15 TO 19	20 TO 24	25 TO 29	30 TO 34	35 TO 39	40 TO 44	45 TO 49	50 TO 54	55 TO 59	60 TO 64	65 TO 69	70 TO 74	75 TO 79	80 TO 84	85 TO 89	90 TO 94	95 TO 99	100 AND ABOVE	PRD. BEGINS						
MAY 11									11	56	156	211	144	122	78	89	89	22	11	11			MAY 11						
MAY 11								10	10	41	92	133	163	194	163	173	20						MAY 11						
MAY 21										8	92	153	137	168	160	130	130	23					MAY 21						
JUN 1										30	65	75	140	180	200	155	95	50					JUN 1						
JUN 11											35	130	135	145	160	160	120	80	30		5		JUN 11						
JUN 21										5	45	85	136	166	186	161	131	55	25		5		JUN 21						
JUL 1											10	55	85	75	145	120	250	135	110		15		JUL 1						
JUL 11												15	65	105	180	205	240	125	55		10		JUL 11						
JUL 21									5	9	23	36	73	123	186	305	214	23			5		JUL 21						
AUG 1											15	40	15	95	210	215	200	175	20		15		AUG 1						
AUG 11										10	15	50	60	75	140	235	230	120	65				AUG 11						
AUG 21										23	73	82	118	177	177	141	91	73	45				AUG 21						
SEP 1										10	45	40	90	115	160	175	170	145	50				SEP 1						
SEP 11									5	20	61	136	141	131	126	152	157	61	5		5		SEP 11						
SEP 21										61	96	131	126	162	131	121	71	81	20				SEP 21						
OCT 1										19	126	117	155	126	146	107	165	39					OCT 1						
OCT 11										29	157	257	214	157	100	43	43						OCT 11						
OCT 21									26	169	208	260	117	91	104	26							OCT 21						
MONTH																							MONTH						
MAY									6	19	60	125	144	141	150	141	132	66	13	3			MAY						
JUN										12	48	97	137	164	182	159	115	62	22		3		JUN						
JUL											5	21	40	58	106	140	213	229	152		31		JUL						
AUG											11	35	58	66	118	176	195	171	121		44	5	AUG						
SEP									2	30	67	102	119	136	139	149	133	96	25		2		SEP						
OCT									8	68	160	200	160	124	120	64	80	16					OCT						

RELATIVE HUMIDITY

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER			KINGSTON RS																	HUMIDITY VALUES										1951-1970											
			0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100																		
PRD.	TO	4	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	PRD.	TO																	
BEGINS	4	9	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99		BEGINS	4																	
MAY 1					78	133	78	33	78	156	44	111	56	33	33	33	44	33	56				MAY 1																		
MAY 11					61	102	194	163	102	133	71	31	10	10	10	10	51	10	31	10			MAY 11																		
MAY 21				8	31	69	237	130	107	99	76	38	53	31		31	31	8	31	23			MAY 21																		
JUN 1			5	5	20	45	130	120	155	105	70	60	35	60	45	40	25	35	50				JUN 1																		
JUN 11			5		40	80	120	160	80	130	65	90	70	40	10	15	30	15	25	25			JUN 11																		
JUN 21					25	80	136	176	131	95	75	50	50	25	35	30	15	40	25	10			JUN 21																		
JUL 1					60	145	210	170	115	55	55	30	45	30	5	30	20	10	15	5			JUL 1																		
JUL 11				10	80	225	220	205	90	60	50	20		15	10	10	5						JUL 11																		
JUL 21				45	200	295	218	100	50	18	18		14	14	5		14		9				JUL 21																		
AUG 1		5	55	55	220	185	155	120	85	40	40	20	5	25	10	15	5	10			5		AUG 1																		
AUG 11			95	180	255	170	80	60	25	25	15	20	10	15	10	15	10	10	5				AUG 11																		
AUG 21			77	141	132	141	123	59	55	50	50	32	18	14	32	14	23	41					AUG 21																		
SEP 1			30	120	180	185	145	90	70	55	5	25	20		15	5	15	15	20			5	SEP 1																		
SEP 11			15	66	146	177	106	86	71	56	40	15	25	30	30	45	5	45	40				SEP 11																		
SEP 21		5	5	56	152	116	116	86	66	91	51	45	30	30	25	30	25	30	40				SEP 21																		
OCT 1				49	78	136	87	146	78	87	39	10	58	49	58	39	10	39	39				OCT 1																		
OCT 11					14	57	143	143	186	114	57	43	29	43	29	29	29	43	29	14			29	OCT 11																	
OCT 21						13	26	117	104	91	78	91	117	13	78	52	52	26	130			13		OCT 21																	
MONTH																							MONTH																		
MAY				3	53	97	179	113	97	125	66	56	41	25	13	25	41	16	38	13				MAY																	
JUN				3	28	68	129	152	122	110	70	67	52	42	30	28	23	30	33	12				JUN																	
JUL				19	116	224	216	156	84	44	40	16	19	19	6	13	13	3	8	2				JUL																	
AUG		2	76	179	189	155	108	68	40	39	29	19	18	13	19	11	15	18	3				AUG																		
SEP		2	17	81	159	159	122	87	69	67	32	29	25	20	23	27	15	30	34			2	SEP																		
OCT					20	36	76	84	136	116	96	56	44	58	36	56	40	32	32	60			12	OCT																	

(con.)

Table 12 (Con.)

DRY BULB TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100306 MT COUER D ALENE LO																		1954-1970									
		TEMPERATURE VALUES																											
PRD.	BELOW	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	PRD.						
BEGINS	0	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99	AND ABOVE	BEGINS						
JUL 1										13	13	34	60	94	174	262	141	168	40				JUL 1						
JUL 11												6	65	76	135	224	194	182	106	12			JUL 11						
JUL 21											5	27	43	64	96	176	198	262	112	16			JUL 21						
AUG 1											6	35	41	88	171	182	200	165	82	12	18		AUG 1						
AUG 11											25	25	43	74	123	215	245	98	104	49			AUG 11						
AUG 21											31	23	101	124	163	155	147	109	101	39	8		AUG 21						
MONTH																				MONTH									
JUL										4	6	22	55	77	132	217	180	208	89	10			JUL						
AUG											19	28	58	93	152	186	201	126	95	32	9		AUG						

RELATIVE HUMIDITY

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100306		MT COUER D ALENE LO																		1954-1970											
		HUMIDITY VALUES																															
PRD.		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100			PRD.								
BEGINS		TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO			BEGINS								
		4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99												
JUL 1					20	40	107	148	161	114	141	87	40	20	13	20	27	34		13			13		JUL 1								
JUL 11					41	76	141	182	118	147	100	65	41	29	24	6	12		18						JUL 11								
JUL 21					5	43	176	251	155	118	91	37	32	5	11	16	5	16	11	5	5	16			JUL 21								
AUG 1					18	88	176	147	118	135	59	41	65	53	6	12	29	12	6	18	18				AUG 1								
AUG 11			6		31	104	160	166	190	67	86	25	31	25	18	31	6	12		25	18				AUG 11								
AUG 21					47	109	140	140	101	147	54	78	8	23	23	23	39	8	23	8	31				AUG 21								
MONTH																								MONTH									
JUL					2	36	103	172	162	130	117	89	59	28	20	18	10	18	14	8	6	10			JUL								
AUG			2		30	100	160	152	139	115	67	45	37	35	15	22	24	6	11	4	24	13			AUG								

DRY BULB TEMPERATURE

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100417		SPYGLASS LO																		1951-1970									
				TEMPERATURE VALUES																											
PRD.	BELOW	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100			PRD.						
BEGINS	0	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84	89	94	99	ABOVE			BEGINS						
JUL 1										13	67	73	73	187	167	220	113	80	7						JUL 1						
JUL 11												10	55	101	191	206	196	101	35	5					JUL 11						
JUL 21									5		23	50	45	55	191	214	291	114	14						JUL 21						
AUG 1										10	25	30	70	110	165	220	235	105	15	10	5				AUG 1						
AUG 11										10	26	67	41	108	144	206	222	113	62						AUG 11						
AUG 21									7	14	75	88	122	170	184	82	109	68	82						AUG 21						
MONTH																															
JUL										2	4	30	58	72	105	185	213	211	100	19	2				JUL						
AUG										2	11	39	59	74	126	163	177	196	98	50	4	2			AUG						

RELATIVE HUMIDITY

PERCENTAGE FREQUENCY DISTRIBUTION OF DAILY VALUES
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER		100417		SPYGLASS LO																		1951-1970									
				HUMIDITY VALUES																											
PRD. BEGINS		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	PRD. BEGINS								
		TO 4	TO 9	TO 14	TO 19	TO 24	TO 29	TO 34	TO 39	TO 44	TO 49	TO 54	TO 59	TO 64	TO 69	TO 74	TO 79	TO 84	TO 89	TO 94	TO 99										
JUL 1					7	13	107	107	167	127	67	67	67	40	67	53	13	27	33	20		20	JUL 1								
JUL 11					20	40	70	151	196	136	116	60	60	25	50	15	30	5	15	5		5	JUL 11								
JUL 21					32	105	105	205	223	95	73	45	32	9	9	5	9	9	18	18		9	JUL 21								
AUG 1					5	60	120	130	125	145	70	55	85	30	20	25	15	15	20	10		15	AUG 1								
AUG 11					5	31	67	119	191	149	124	62	67	46	5	26	15	10	21	10	10	31	AUG 11								
AUG 21					27	68	116	116	102	68	102	68	82	54	14	14	34	14	20	20	34	48	AUG 21								
MONTH																						MONTH									
JUL					21	58	93	160	199	118	86	56	51	23	39	21	18	12	21	14		11	JUL								
AUG					2	20	65	118	148	128	116	76	63	70	37	24	17	22	17	15	17	30	AUG								

Table 13--Windspeed (miles per hour) averages and frequencies by wind direction; data observed near 1500 P.s.t. For months of fire season, for indicated years of record, mostly 1954-70

WIND SPEED - DIRECTION
PERCENTAGE FREQUENCY OF OCCURRENCE BY DIRECTION FOR SELECTED SPEED INCREMENTS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100304 FERNAN RS

1954-1970

MONTH MAY										MONTH JUN									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	I	DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	I
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	I	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	I
NE	2	5	1	2			5	12	5.6	I	4	0	9	19	2	4	15	32	5.1
E	12	29	7	17			19	46	3.2	I	6	13	5	11			11	23	3.7
SE	14	34	10	24	3	7	27	66	4.1	I	16	34	9	19	3	6	28	59	4.0
S	32	78	62	150	16	39	112	272	5.2	I	21	44	74	156	19	40	117	247	5.6
SW	43	104	45	109	13	32	105	255	5.0	I	21	44	51	108	23	49	102	216	6.4
W	29	70	44	107	14	34	89	216	5.2	I	35	74	59	125	35	74	133	281	6.0
NW	10	24	8	19	2	5	20	49	4.4	I	13	27	22	47	3	6	39	82	5.0
N	22	53	7	17	2	5	31	75	2.9	I	12	25	13	27	2	4	27	57	4.4
CLM	4	10					4	10	0.0	I	1	2					1	2	0.0
TOT	168	408	185	449	51	124	412	4.7	I	129	273	242	512	87	184	13	473	5.6	
MONTH JUL										MONTH AUG									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	I	DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	I
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	I	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	I
NE	3	6	1	2			10	19	4.9	I	6	11	2	4	1	2	9	17	3.4
E	6	11	15	29	2	4	23	44	4.6	I	8	15	5	10			13	25	3.5
SE	8	15	15	29	5	10	30	57	5.9	I	8	15	11	21	1	2	20	38	4.1
S	27	52	93	178	18	34	141	270	5.3	I	28	53	61	116	24	46	114	218	5.4
SW	21	40	84	161	27	52	134	256	5.7	I	27	52	73	139	29	55	133	254	6.0
W	14	27	68	130	26	50	113	216	6.2	I	36	69	95	181	36	69	173	330	5.7
NW	10	19	28	54	2	4	42	80	4.8	I	11	21	28	53	6	11	45	86	5.0
N	14	27	13	25			27	52	3.6	I	9	17	6	11	2	4	17	32	4.1
CLM	3	6					3	6	0.0	I									
TOT	106	203	322	616	81	155	523	5.5	I	133	254	281	536	99	189	10	524	5.4	
MONTH SEP										MONTH OCT									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	I	DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	I
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	I	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	I
NE	7	14	6	12	10	20	23	47	6.1	I	5	15	3	9			8	23	3.4
E	10	20	5	10	1	2	16	33	3.6	I	8	23	10	29			18	53	3.6
SE	16	33	5	10	3	6	24	49	3.5	I	15	44	7	20	1	3	23	67	3.2
S	48	98	48	98	13	27	110	225	4.5	I	56	164	26	76	6	18	88	257	3.4
SW	37	76	48	98	15	31	104	213	5.1	I	37	108	39	114	13	38	96	287	5.5
W	43	88	56	115	20	41	127	260	5.7	I	33	96	19	56	9	26	63	184	4.6
NW	15	31	23	47	5	10	44	90	4.8	I	17	50	9	26	1	3	28	82	3.9
N	18	37	18	37	2	4	38	78	3.9	I	6	18	5	15	1	3	12	35	4.1
CLM	3	6					3	6	0.0	I	4	12					4	12	0.0
TOT	197	403	209	427	69	141	489	4.9	I	181	529	118	345	31	91	11	342	4.2	

(con.)

Table 13 (Con.)

W I N D S P E E D - D I R E C T I O N
PERCENTAGE FREQUENCY OF OCCURRENCE BY DIRECTION FOR SELECTED SPEED INCREMENTS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED-

STATION NUMBER 100409 KINGSTON RS

1954-1970

MONTH MAY										MONTH JUN									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		
N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT
NE	17	70	10	41	2	8	29	120	3.6	18	38	35	74	4	8	57	121	4.3	
E	10	41	5	21			15	62	3.1	15	32	15	32	2	4	32	68	4.0	
SE	6	25	9	37		8	17	70	4.2	15	32	10	21	2	4	27	57	3.9	
S	3	12	6	25	2	8	11	45	5.5	6	13	11	23	2	4	19	40	4.5	
SW	9	37	21	67	4	17	34	140	4.8	10	21	11	23	1	2	22	47	3.7	
W	8	33	12	50			20	83	4.0	41	97	22	47			63	133	3.1	
NW	28	116	51	211	4	17	83	343	4.2	62	131	67	142	4	6	133	282	3.8	
CLM	13	54	18	74	1	4	32	132	3.8	48	102	62	131	3	6	114	242	4.1	
CLM	1	4					1	4	0.0	5	11					5	11	0.0	
TOT	95	393	132	545	15	62	242		4.1	220	466	233	494	18	38	472		3.8	
MONTH JUL										MONTH AUG									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		
N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT
NE	25	49	27	53	4	8	56	110	3.8	21	41	37	72			58	113	3.9	
E	23	45	19	37			42	82	3.5	18	35	20	39			39	76	3.8	
SE	10	20	5	10	1	2	16	31	3.6	11	21	9	18	2	4	22	43	3.7	
S	8	16	11	22	2	4	21	41	4.3	4	8	4	8			8	16	3.4	
SW	17	33	17	33	2	4	36	70	4.0	17	33	15	29	1	2	33	64	3.6	
W	38	74	37	72			75	147	3.6	33	64	51	90	2	4	86	167	3.9	
NW	68	133	93	182			164	321	3.9	58	113	86	167	3	6	147	286	3.9	
CLM	38	74	56	110	2	4	96	188	4.0	43	84	71	138	4	8	118	230	4.0	
CLM	5	10					5	10	0.0	3	6					3	6	0.0	
TOT	232	454	265	519	14	27	511		3.8	208	405	293	570	12	23	514		3.9	
MONTH SEP										MONTH OCT									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		
N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT	N.	PCT
NE	27	58	22	46			49	106	3.3	15	78	2	10			17	88	2.2	
E	17	37	12	26	1	2	30	65	3.6	6	31					6	31	1.3	
SE	20	43	10	22	1	2	31	67	3.1	17	88	4	21	2	10	23	119	2.9	
S	7	15	5	11			12	26	3.5	2	10	3	16	1	5	6	31	4.3	
SW	26	56	20	43	1	2	47	102	3.5	16	83	5	26	2	10	24	124	3.8	
W	50	108	23	40	3	6	76	164	3.3	27	140	5	26	1	5	33	171	2.4	
NW	32	199	37	80			129	279	2.9	48	249	10	52			58	301	2.4	
CLM	45	97	55	70	1	2	83	179	3.5	14	73	4	21			18	93	2.2	
CLM	6	13					6	13	0.0	8	41					8	41	0.0	
TOT	290	621	164	354	7	15	463		3.2	153	793	33	171	6	31	193		2.5	

(con.)

Table 13 (Con.)

WIND SPEED - DIRECTION
PERCENTAGE FREQUENCY OF OCCURRENCE BY DIRECTION FOR SELECTED SPEED INCREMENTS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100412 MAGEE RS

1963-1972

MONTH JUN										MONTH JUL									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED		N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	
NE	3 13	4 17					7 30	4.4	I	3 11	2 8	1 4	1 4				7 27	5.9	
E	1 4	1 4					2 9	4.0	I		1 4						1 4	5.0	
SE	8 34	11 47	10 43				29 123	6.1	I	5 19	13 50	5 19	1 4				24 92	6.0	
S	44 187	52 221	27 115	I 4			124 528	5.0	I	39 149	69 263	29 111	3 11				140 534	5.3	
SW	8 34	5 21	3 13				16 68	5.0	I	9 34	15 57	4 15	1 4				29 111	5.6	
W	2 9	2 9	2 9				6 26	6.2	I	4 15	1 4	2 8					7 27	4.1	
NW		1 4	2 9	I 4			4 17	8.8	I	2 8	3 11						5 19	4.2	
N	17 72	23 98	7 30				47 200	4.6	I	25 95	16 61	4 15	1 4				46 176	4.1	
CLM									I	3 11							3 11	0.0	
TOT	83 353	99 421	51 217	2 9			235	5.1	I	90 344	120 458	45 172	7 27				262	5.1	

MONTH AUG										MONTH SEP									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED		N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	
NE	4 14	2 7					6 21	3.2	I	5 21	5 21	1 4					11 47	4.5	
E	2 7	2 7	1 3				5 17	4.0	I	2 8							2 8	2.0	
SE	8 28	20 70	5 17				34 119	5.9	I	5 21	7 30	6 25	1 4				19 81	6.3	
S	58 203	76 266	20 70	3 10			157 549	4.8	I	53 225	52 220	20 85	2 8				127 538	4.5	
SW	6 21	15 52	5 17				26 91	5.2	I	18 76	11 47	7 30	2 8				38 161	5.1	
W									I	1 4	1 4						2 8	3.5	
NW	3 10	1 3					4 14	3.3	I	1 4	3 13						4 17	4.8	
N	22 77	21 73	7 24	1 3			51 178	4.6	I	19 81	8 34	3 13					30 127	3.5	
CLM	3 10						3 10	0.0	I	3 13							3 13	0.0	
TOT	106 371	137 479	38 133	4 14	1 3		286	4.8	I	107 453	87 369	37 157	5 21				236	4.5	

WIND SPEED - DIRECTION
PERCENTAGE FREQUENCY OF OCCURRENCE BY DIRECTION FOR SELECTED SPEED INCREMENTS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100306 MT COEUR D'ALENE LO

1954-1970

MONTH JUL										MONTH AUG									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED		N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	
NE	4 8		4 8				8 16	5.4	I	8 18	7 16						15 34	3.6	
E	3 6	6 12	2 4				11 23	5.0	I	4 9	5 11						9 21	3.7	
SE	5 10	4 8					9 18	3.6	I	2 5	6 14	1 2					4 21	4.6	
S	30 61	32 66	11 23	I 2			74 152	4.6	I	12 28	22 51	9 21		2 5			45 103	5.8	
SW	77 158	116 238	51 105	6 12			250 512	5.4	I	47 108	138 317	57 131	3 7	1 2			246 566	5.8	
W	20 41	26 53	4 8	1 2			51 105	4.7	I	14 32	11 25	4 9					29 67	4.2	
NW	15 31	33 68	3 6				51 105	4.6	I	18 41	30 69	5 11					53 122	4.5	
N	8 16	12 25	3 6				23 47	4.9	I	9 21	12 28	1 2					22 51	4.0	
CLM	11 23						11 23	0.0	I	7 16							7 16	0.0	
TOT	174 355	229 469	78 160	8 16			488	4.9	I	121 278	231 531	77 177	5 11	1 2			435	5.2	

WIND SPEED - DIRECTION
PERCENTAGE FREQUENCY OF OCCURRENCE BY DIRECTION FOR SELECTED SPEED INCREMENTS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100417 SPYGLASS LO

1954-1970

MONTH JUL										MONTH AUG									
WIND SPEED, MPH										WIND SPEED, MPH									
DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG		DIR.	0-3	4-7	8-12	13-18	19-24	>24	TOTAL	AVG	
N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED		N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	N. PCT	SPEED	
NE	18 37	12 25	2 4				32 66	3.6	I	7 16	11 25	1 2					19 43	4.9	
E	2 4	6 12					8 16	3.8	I	5 11	3 7						8 18	3.3	
SE	5 10	8 16					13 27	3.5	I	5 11	7 16	2 5					14 32	4.9	
S	7 14	16 33	5 10	1 2			29 60	5.6	I	4 9	10 23	6 14					20 45	5.9	
SW	38 78	129 266	85 175	10 21			263 542	6.6	I	36 82	128 290	92 209	11 25	2 5			269 610	7.0	
W	20 41	46 95	21 43	4 8			91 188	6.1	I	17 39	38 86	21 48					76 172	5.9	
NW	21 43	10 21	1 2				32 66	3.2	I	15 34	11 25						26 59	3.6	
N	6 12	6 12	1 2				13 27	3.4	I	3 7	1 2						4 8	3.3	
CLM	4 8						4 8	0.0	I	5 11							5 11	0.0	
TOT	121 249	233 480	115 237	15 31		1 2	485	5.8	I	97 220	209 474	122 277	11 25	2 5			441	6.2	

Table 14--Frequencies of three-way combinations of dry bulb (degrees Fahrenheit), relative humidity (percent), and windspeed (miles per hour); data observed near 1500 P.s.t. For months of fire season, for indicated years of record

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS

-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100304

FERNANDES

1954-1970

MONTH MAY

222

WIND SPEED 0-4 MPH											WIND SPEED 5-9 MPH											WIND SPEED 10-14 MPH										
RELATIVE HUMIDITY											RELATIVE HUMIDITY											RELATIVE HUMIDITY										
TEMP. DEG F	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		
<100																																
95-99																																
90-94																																
85-89	2	9	11	7								2		9	2								2									
80-84		7	25	5								5	9	7	2									2								
75-79	2	5	37	28	5							2	21	7	2									2								
70-74		5	14	28	14	7						5	25	21	7								2	2	2	5						
65-69			11	18	18	7	5	2				2	14	18	21	11	2							2	5		7	2				
60-64		2	5	14	34	16	2	2				2	7	21	21	7	11							5				2				
55-59			9	5	18	9	9	11	14	2			2	9	14	14		5		2		2		5			5	2		2		
50-54				2		7	7	23	14	1				9	21	5	14	7									5	2				
45-49					5		2	7	7	9	1			2			5		7				2				5					
40-44									5	7	1						2	2	2													
35-39										2	1																					
30-34											1																					
<30											1																					
TOTAL	5	28	120	103	103	48	28	30	48	34	1	18	78	87	78	53	18	25	9	11	1	5	14	9	21	11	5			2		
NUMBER	2	12	52	45	45	21	12	13	21	15	1	0	8	34	38	34	23	8	11	4	5	1	0	2	6	4	9	5	2	0	1	

WIND SPEED 15-19 MPH											WIND SPEED GREATER/EQUAL 20 MPH											TOTAL		NUMBER		
<100																							0			
95-99																							0			
90-94																							7			
85-89																							34			
80-84																							57			
75-79																							110			
70-74																							131			
65-69	2																						147			
60-64																							161			
55-59	2																						138			
50-54											2												140			
45-49																							51			
40-44																							21			
35-39																							2			
30-34																										
<30																							0			
TOTAL	2										2										1000					
NUMBER	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1			435		

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS - GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																																		
STATION NUMBER 100304										FLRNNR S										1954-1970														
MONTH JUN																																		
WIND SPEED 0-4 MPH										WIND SPEED 5-9 MPH										WIND SPEED 10-14 MPH														
RELATIVE HUMIDITY										RELATIVE HUMIDITY										RELATIVE HUMIDITY														
TEMP, DEG F	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100				
<100																																		
95-99																																		
90-94																																		
85-89		6	18										2	4																				
80-84		10	8	6									4	29	6																			
75-79		2	35	18	8								8	29	29	4																		
70-74		2	16	22	2	2							43	24	14	2																		
65-69			18	18	22	4							6	20	41	22	4	2																
60-64			2	12	22	16	4	8	8	2			6	27	20	10	8			2														
55-59				6	14	18	6	8	8	8				10	24	12	6	5	5															
50-54					6	2	18							2	2	6	4	2	4															
45-49					2	2			10	12						4	2		2	6														
40-44								2		2									4	2														
35-39																																		
30-34																																		
<30																																		
TOTAL	20	98	84	65	45	24	35	27	24				22	141	139	88	39	22	8	10	10				6	18	20	18	8	2	4			
NUMBER	0	10	48	41	32	22	12	17	13	12			0	11	69	68	43	19	11	4	5	5			0	3	9	10	9	4	1	2	0	0
WIND SPEED 15-19 MPH										WIND SPEED GREATER/EQUAL 20 MPH										TOTAL NUMBER														
<100																																		
95-99																																		
90-94																																		
85-89																																		
80-84																																		
75-79																																		
70-74																																		
65-69																																		
60-64																																		
55-59																																		
50-54																																		
45-49																																		
40-44																																		
35-39																																		
30-34																																		
<30																																		
TOTAL		4	6	2		4			2						2																			
NUMBER	0	2	3	1	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																																																
STATION NUMBER 100304															FERNAN RS															1954-1970																		
MONTH JUL ---																																																
WIND SPEED 0-4 MPH															WIND SPEED 5-9 MPH															WIND SPEED 10-14 MPH																		
RELATIVE HUMIDITY															RELATIVE HUMIDITY															RELATIVE HUMIDITY																		
TEMP. DEG F	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	I	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	I	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	I	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100					
<100			2								I			4								I											I															
95-99		27	9	2							I		38	6								I											I															
90-94		36	28	9							I	2	70	21	2	2						I											I															
85-89		23	46	9	2						I		47	51	17						I												I															
80-84		9	32	34	6	2					I		13	44	28	8					I												I															
75-79		4	8	21	4	2					I		2	46	27	2					I												I															
70-74			4	11	15	2	8				I			2	30	8	4				I												I															
65-69				4	8	9	2				I				4	8	4	4				I												I														
60-64						2	4	8	4		I					2	2	8				I												I														
55-59						2		2	4		I											I												I														
50-54											I											I												I														
45-49											I											I												I														
40-44											I											I												I														
35-39											I											I												I														
30-34											I											I												I														
<30											I											I												I														
TOTAL		99	129	91	34	19	13	9	8		I	2	175	169	110	28	9	11	6	4	6	I											I															
NUMBER	0	52	68	48	18	10	7	5	4	0	I	1	92	89	58	15	5	6	3	2	3	I	0	13	9	8	3	0	1	0	0	0	I															
WIND SPEED 15-19 MPH															WIND SPEED GREATER/EQUAL 20 MPH															TOTAL										NUMBER								
<100											I											I											I															
95-99											I											I											I															
90-94		2	2								I			2								I											I															
85-89		2									I											I											I															
80-84											I											I											I															
75-79											I											I											I															
70-74											I											I											I															
65-69					2						I											I											I															
60-64											I											I											I															
55-59											I											I											I															
50-54								2			I											I											I															
45-49											I											I											I															
40-44											I											I											I															
35-39											I											I											I															
30-34											I											I											I															
<30											I											I											I															
TOTAL		4	2	2	2			2			I			2								I											I															
NUMBER	0	2	1	1	1	0	0	1	0	0	I	0	0	1	0	0	0	0	0	0	0	I										I																
																																			527													

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																															
STATION NUMBER 100304										FERNAN RS										1954-1970											
MONTH AUG ---																															
WIND SPEED 0-4 MPH										WIND SPEED 5-9 MPH										WIND SPEED 10-14 MPH											
RELATIVE HUMIDITY										RELATIVE HUMIDITY										RELATIVE HUMIDITY											
TEMP. DEG F	1 TO	11 TO	21 TO	31 TO	41 TO	51 TO	61 TO	71 TO	81 TO	91 TO	1 TO	11 TO	21 TO	31 TO	41 TO	51 TO	61 TO	71 TO	81 TO	91 TO	1 TO	11 TO	21 TO	31 TO	41 TO	51 TO	61 TO	71 TO	81 TO	91 TO	
	10	20	30	40	50	60	70	80	90	100	10	20	30	40	50	60	70	80	90	100	10	20	30	40	50	60	70	80	90	100	
<100	9	2									9	6																			
95-99	8	28	2								2	32	4																		
90-94	2	46	19									42	8																		
85-89		32	38	11							2	47	27		2																
80-84		11	36	21	4							11	68	15	2																
75-79		4	17	25	8			2				8	25	27																	
70-74			11	8	9	8	2					2	11	25	19	6															
65-69				2	4	6	11	8					2	11	6	2	2	4													
60-64					8	4		8	4	2	1			4	4	6	6	2	4												
55-59							4	9	6	2	1																				
50-54									4	2	1																			2	
45-49										1																					
40-44										1																					
35-39										1																					
30-34										1																					
<30										1																					
TOTAL	19	123	123	66	32	19	19	25	13	6	1	13	148	144	82	32	15	9	8	6	1		27	32	9	9	4	4	2	2	
NUMBER	10	65	65	35	17	10	10	13	7	3	1	7	78	76	43	17	8	5	4	3	0	1	0	14	17	5	5	2	2	1	1
WIND SPEED 15-19 MPH										WIND SPEED GREATER/EQUAL 20 MPH										TOTAL NUMBER											
<100										1											1	27	14								
95-99										1											1	76	40								
90-94		2								1											1	123	65								
85-89										1											1	184	97								
80-84			2							1											1	190	100								
75-79				2						1											1	131	69								
70-74					2					1											1	112	59								
65-69										1											1	61	32								
60-64										1											1	59	31								
55-59										1											1	28	15								
50-54										1											1	9	5								
45-49										1											1		0								
40-44										1											1		0								
35-39										1											1		0								
30-34										1											1		0								
<30										1											1		0								
TOTAL		2	4	2						1											1	1000									
NUMBER	0	1	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1		527								

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS

-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100304

FERNAN RS

1954-1970

MONTH SEP

...

WIND SPEED 0-4 MPH											WIND SPEED 5-9 MPH											WIND SPEED 10-14 MPH										
RELATIVE HUMIDITY											RELATIVE HUMIDITY											RELATIVE HUMIDITY										
TEMP.	1	11	21	31	41	51	61	71	81	91	1	1	11	21	31	41	51	61	71	81	91	1	1	11	21	31	41	51	61	71	81	91
DEG F	10	20	30	40	50	60	70	80	90	100	1	10	20	30	40	50	60	70	80	90	100	1	10	20	30	40	50	60	70	80	90	100
<100											1											1										
95-99											1											1										
90-94											1											1										
85-89											1											1										
80-84											1											1										
75-79											1											1										
70-74											1											1										
65-69											1											1										
60-64											1											1										
55-59											1											1										
50-54											1											1										
45-49											1											1										
40-44											1											1										
35-39											1											1										
30-34											1											1										
<30											1											1										
TOTAL											1											1										
NUMBER	0	37	100	58	30	24	16	12	11	12	1	1	17	50	41	27	8	5	7	3	3	1	0	4	12	6	4	7	3	2	2	

	WIND SPEED 15-19 MPH										WIND SPEED GREATER/EQUAL 20 MPH										TOTAL	NUMBER
<100																				0		
95-99																		5		3		
90-94																		37		19		
85-89																		94		48		
80-84	2																	118		60		
75-79				2														161		82		
70-74				2														133		68		
65-69				4														159		81		
60-64						2												116		59		
55-59								2										106		54		
50-54														2				53		27		
45-49																		12		6		
40-44																		5		3		
35-39																				0		
30-34																				0		
<30																				0		
TOTAL		2	6	2		2								2					1000			
NUMBER	0	1	3	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	510	

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100304

FERNAN RS

1954-1970

MONTH OCT

TEMP. DEG F	WIND SPEED 0-4 MPH										I	WIND SPEED 5-9 MPH										I	WIND SPEED 10-14 MPH										I		
	RELATIVE HUMIDITY											RELATIVE HUMIDITY											RELATIVE HUMIDITY												
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100			
<100											I											I												I	
95-99											I											I												I	
90-94											I											I												I	
85-89											I											I												I	
80-84		3	8								I		3									I												I	
75-79		3	10	18							I		10	3								I												I	
70-74			5	26	18	3					I		13	3	3							I			3									I	
65-69		3	10	28	23	10					I		5	3	21							I						3						I	
60-64		3	5	23	26	26	13	5			I		5	5	8	8						I												I	
55-59			5	21	28	10	36	26	10	3	I		3	3	10	5		8			3	I						3	3	3	3	5	3		I
50-54			3	10	18	38	38	15	36	5	I		5	13	5	21	3	5	5	5	8	I					3	5							I
45-49				3	5	13	18	15	21	15	I				3	3	5	15	5	8	I						3	3							I
40-44			3				5	5	13	23	I						5				3	I													I
35-39										8	I											I													I
30-34										3	I											I													I
<30										3	I											I													I
TOTAL	10	49	128	118	100	110	64	85	54		I	3	38	28	49	36	13	28	10	21	I		3	5	5	5	8	8	5			3		I	
NUMBER	0	4	19	50	46	39	43	25	33	21	I	0	1	15	11	19	14	5	11	4	8	I	0	1	2	2	2	3	3	2	0		1		
	WIND SPEED 15-19 MPH										I	WIND SPEED GREATER/EQUAL 20 MPH										I	TOTAL		NUMBER										
<100											I											I			0										
95-99											I											I			0										
90-94											I											I			0										
85-89											I											I			0										
80-84											I											I	13		5										
75-79											I											I	46		18										
70-74											I											I	72		28										
65-69							3				I											I	105		41										
60-64						3					I											I	128		50										
55-59			3								I											I	185		72										
50-54							3	3			I											I	241		94										
45-49									3		I											I	138		54										
40-44											I											I	59		23										
35-39											I											I	8		3										
30-34											I											I	3		1										
<30											I											I	3		1										
TOTAL				3	5	5	3				I											I	1000												
NUMBER	0	0	0	1	2	2	1	0	0	0	I	0	0	0	0	0	0	0	0	0	0	I			390										

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
 PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
 -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100409

KINGSTON RS

1954-1970

MONTH: JUN

TEMP. DEG F	WIND SPEED 0-4 MPH										I	WIND SPEED 5-9 MPH										I	WIND SPEED 10-14 MPH										I
	RELATIVE HUMIDITY											RELATIVE HUMIDITY											RELATIVE HUMIDITY										
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	
<100										I											I										I		
95-99				4						I											I										I		
90-94		6	16							I		2	2								I										I		
85-89		12	22							I		4	20	6							I										I		
80-84		2	43	29	8	2				I		2	20	12	2	2					I					2	2				I		
75-79		4	27	43	12	2				I		2	18	27	14						I										I		
70-74		4	22	43	20	20	2			I		20	25	16	4	2					I					4	2				I		
65-69			8	22	43	14	10	4	2	I		6	25	12	8	2	2				I										I		
60-64				12	22	22	14	16	10	I			6	14	10	2	2				I										I		
55-59				2	12	12	24	18	14	6 I			2		6			2			I										I		
50-54						4	2	8	22	8 I					2				2		I										I		
45-49							2		8	I											I										I		
40-44										I											I											I	
35-39										I											I											I	
30-34										I											I											I	
<30										I											I											I	
TOTAL		27	141	157	118	75	53	45	55	14 I		10	84	104	57	31	6	8	2		I				8	4						I	
NUMBER	0	14	72	80	60	38	27	23	28	7 I	0	5	43	53	29	16	3	4	1	0	I	0	0	4	2	0	0	0	0	0	0	0	I

WIND SPEED 15-19 MPH											I	WIND SPEED GREATER/EQUAL 20 MPH											I	TOTAL	NUMBER
-----											I	-----											I		
											I												I		0
<100											I												I		2
95-99											I												I	4	2
90-94											I												I	25	13
85-89											I												I	71	36
80-84											I												I	125	64
75-79											I												I	153	78
70-74											I												I	180	92
65-69											I												I	161	82
60-64											I												I	127	65
55-59											I												I	96	49
50-54											I												I	47	24
45-49											I												I	10	5
40-44											I												I		0
35-39											I												I		0
30-34											I												I		0
<30											I												I		0
-----											I	-----											I		
TOTAL											I												I	1000	
											I												I		
NUMBER	0	0	0	0	0	0	1	0	0	0	I	0	0	0	0	0	0	0	0	0	0	I			510

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED																																								
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS																																								
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED																																								
STATION NUMBER 100409										KINGSTON RS										1954-1970																				
MONTH JUL																																								

WIND SPEED 0-4 MPH										WIND SPEED 5-9 MPH										WIND SPEED 10-14 MPH																				
RELATIVE HUMIDITY										RELATIVE HUMIDITY										RELATIVE HUMIDITY																				
1	11	21	31	41	51	61	71	81	91	1	11	21	31	41	51	61	71	81	91	1	11	21	31	41	51	61	71	81	91	1	11	21	31	41	51	61	71	81	91	
TEMP.	TO	TO	TO	TO	TO	TO	TO	TO	TO	TEMP.	TO	TO	TO	TO	TO	TO	TO	TO	TO	TEMP.	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	
DEG F	10	20	30	40	50	60	70	80	90	100	10	20	30	40	50	60	70	80	90	100	10	20	30	40	50	60	70	80	90	100	10	20	30	40	50	60	70	80	90	100

<100										2																														
95-99										17 9																														
90-94										40 59 6 4																														
85-89										32 110 27 2										2																				
80-84										11 66 53 9										2																				
75-79										27 25 17 2 2																														
70-74										6 32 13 8 2 2																														
65-69										4 21 9 8 2																														
60-64										2 4 9 13 8 6																														
55-59										2 9 4 2 1																														
50-54										4 2																														
45-49										4 2																														
40-44										1																														
35-39										1																														
30-34										1																														
<30										1																														

TOTAL										101 281 146 72 28 27 25 11 2										65 133 76 21 6 4 2 2																				

NUMBER										0 53 148 77 38 15 14 13 6 1										7 34 70 40 11 0 3 2 0 0 0 1 1 0 0 0 0 0 0 0 0																				

WIND SPEED 15-19 MPH										WIND SPEED GREATER/EQUAL 20 MPH										TOTAL NUMBER																				

<100																				6 3																				
95-99																				34 18																				
90-94																				144 76																				
85-89																				220 116																				
80-84																				216 114																				
75-79																				140 74																				
70-74																				102 54																				
65-69																				65 34																				
60-64																				44 23																				
55-59																				23 12																				
50-54																				6 3																				
45-49																				0																				
40-44																				0																				
35-39																				0																				
30-34																				0																				
<30																				0																				

TOTAL																				1000																				

NUMBER										0 0 0 0 0 0 0 0 0 0										0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0																				

																				527																				

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100409

KINGSTON RS

1954-1970

MONTH AUG

TEMP. DEG F	WIND SPEED 0-4 MPH										I	WIND SPEED 5-9 MPH										I	WIND SPEED 10-14 MPH										I
	RELATIVE HUMIDITY											RELATIVE HUMIDITY											RELATIVE HUMIDITY										
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100			
<100	4										2																						
95-99	2	23	4								15	2																					
90-94		65	28								17	4																					
85-89		65	46	8							27	27																					
80-84		34	47	21	2	2					19	53	8																				
75-79		8	49	38	15	4					4	32	30																				
70-74			11	30	25	6	4				2	9	17	9	2		2																
65-69			2	13	8	19	4	8	2			2		8	4																		
60-64					8	8	13	8	8	2			2	2	4	4	2																
55-59					6		4	9	15					2				2	2														
50-54									8	2																							
45-49																																	
40-44																																	
35-39																																	
30-34																																	
<30																																	
TOTAL	6	194	188	110	63	38	25	25	32	4		85	129	57	21	9	4	6	4														
NUMBER	3	102	99	58	33	20	13	13	17	2		0	45	68	30	11	5	2	3	2	0		0	0	0	0	0	0	0	0			

TEMP.	WIND SPEED 15-19 MPH										I	WIND SPEED GREATER/EQUAL 20 MPH										I	TOTAL							
	RELATIVE HUMIDITY											RELATIVE HUMIDITY											NUMBER							
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100
<100																														
95-99																														
90-94																														
85-89																														
80-84																														
75-79																														
70-74																														
65-69																														
60-64																														
55-59																														
50-54																														
45-49																														
40-44																														
35-39																														
30-34																														
<30																														

(con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
WT. DECIMAL POINT OMITTED

1954-1970

KINGSTON RS

...

1

I

4 MPH

RELATIVE HUMIDITY

RELATIVE HUMIDITY

[illegible]

TOTAL	2	82	267	169	122	41	35	51	35	33	1	16	39	43	20	14	12	4	6	6	1	2	2										
NUMBER	1	42	136	86	62	21	18	26	18	17	1	0	8	20	22	10	7	6	2	3	3	1	0	1	1	0	0	0	0	0	0	0	0

WIND SPEED GREATER/EQUAL 20 MPH

TOTAL NUMBER

[illegible]

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WINDSPEED
PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
-GIVEN TO TENTHS PERCENT; DECIMAL POINT OMITTED

STATION NUMBER 100306

MT COVER D ALENE LO

1954-1970

MONTH JUL

TEMP. DEG F	WIND SPEED 0-4 MPH										WIND SPEED 5-9 MPH										WIND SPEED 10-14 MPH									
	RELATIVE HUMIDITY										RELATIVE HUMIDITY										RELATIVE HUMIDITY									
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100
<100																														
95-99																														
90-94			4	4								2	2										2							
85-89		8	34	12							12	43	24	4								4		4						
80-84		6	69	24	16	2					2	38	26	6										6	8	2				
75-79		10	32	30	16	4					2	28	36	32	2									2	8	4	2			
70-74		2	16	42	34	14							8	16	6	2								4		2	2	6		
65-69			6	10	24	12		6			2		24	30	8											2				
60-64				4	2	8	14	8	2				8	16	6	2			2								2			
55-59						6	12	2	2				2	4	6	6		4	8								2			
50-54								2	2										2											4
45-49							4		2									2												2
40-44																		2	2											
35-39								2												2										
30-34																														
<30																														
TOTAL		30	160	121	91	45	30	20	6		18	132	128	91	22	8	10	12	4		6	16	16	10	8					6
NUMBER	0	15	81	61	46	23	15	10	3	0	9	67	65	46	11	4	5	6	2	0	3	8	8	5	4	0	0	0	0	3

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
 PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS

-GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100306

M1 COVER D ALENE LO

1954-1970

MONTH AUG

TEMP. DEG F	WIND SPEED 0-4 MPH										I	WIND SPEED 5-9 MPH										I	WIND SPEED 10-14 MPH										I	
	RELATIVE HUMIDITY											RELATIVE HUMIDITY											RELATIVE HUMIDITY											
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		
<100											I											I											I	
95-99											I			6	2							I											I	
90-94											I		4	13	2							I											I	
85-89			11								I			24	22							I											I	
80-84			28	17	2						I			22	35	4						I											I	
75-79			15	39	6						I			22	35	4						I											I	
70-74			17	52	17	13	2				I			19	37	24						I											I	
65-69			2	30	37	9	4				I			2	43	37	11					I											I	
60-64					37	15	15				I			2	15	19	19	2				I											I	
55-59					11	17	4	9	6		I				2	13	9	6	4	2		I											I	
50-54								2	13		I						9	2	2	6	2	I											I	
45-49						2				4	I						11	2			2	I											I	
40-44										6	I										2	I												I
35-39										11	I										2	I												I
30-34											I											I												I
<30											I											I												I
TOTAL		74	139	110	56	26	11	22		22	I		4	89	158	97	50	30	19	6	9	15	I		6	11	17	4	6	4	2	2		I
NUMBER	0	34	64	51	26	12	5	10	0	10	I	2	41	73	45	23	14	9	3	4	7	I	0	3	5	8	2	3	2	1	1			I

TEMP. DEG F	WIND SPEED 15-19 MPH										I	WIND SPEED GREATER/EQUAL 20 MPH										I	TOTAL NUMBER				
	RELATIVE HUMIDITY											RELATIVE HUMIDITY											I	TOTAL	NUMBER		
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100		1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100						
<100											I											I		0			
95-99											I											I	9	4			
90-94											I											I	32	15			
85-89											I											I	95	44			
80-84											I											I	126	58			
75-79											I											I	201	93			
70-74											I											I	186	86			
65-69											I											I	152	70			
60-64											I											I	93	43			
55-59											I											I	58	27			
50-54											I											I	28	13			
45-49											I											I	19	9			
40-44											I											I		0			
35-39											I											I		0			
30-34											I											I		0			
<30											I											I		0			
TOTAL											I											I	1000				
NUMBER	0	0	0	1	1	0	0	0	2	0	I	0	0	0	0	0	0	0	0	0	0	I		462			

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
 PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
 -GIVEN TO TENTHS PERCENT, DECIMAL POINT OMITTED

STATION NUMBER 100417

SPYGLASS LO

1954-1970

MONTH JUL

TEMP. DEG F	WIND SPEED 0-4 MPH										I	WIND SPEED 5-9 MPH										I	WIND SPEED 10-14 MPH										I			
	RELATIVE HUMIDITY											I	RELATIVE HUMIDITY										I	RELATIVE HUMIDITY										I		
	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90	91 TO 100			1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80	81 TO 90			91 TO 100	1 TO 10	11 TO 20	21 TO 30	31 TO 40	41 TO 50	51 TO 60	61 TO 70	71 TO 80			81 TO 90	91 TO 100
<100											I											I												I		
95-99											I											I												I		
90-94											I		2									I												I		
85-89		8	4	2							I			4	2							I												I		
80-84		4	23	23	2						I		2	25	16	2						I		2		2								I		
75-79		4	35	45	16		2	2			I		8	27	51	8					I			8	4									I		
70-74			8	31	27		6	4			I		2	21	43	23	14				I			4	23		2	2						I		
65-69			8	21	18	10	10	2			I			4	31	37	14	4	2		I				12	6	2							I		
60-64			2	2	8	8	6	8			I			14	14	8	4	4			I				2	8			2	2				I		
55-59				4	2		4	6	8		I			4	6	16	2	6	2		I			2		4								I		
50-54						2	2	2		4	2	I			2	4	4	4	6	14	4	I									2	4		I		
45-49									2	2	6	I						2	2	6	6	I									2	2		I		
40-44											I									2	I													I		
35-39											I										I														I	
30-34											I										I														I	
<30											I										I														I	
TOTAL	16	80	127	74	35	31	21	6	8	1	I	14	80	164	94	57	18	21	25	10	I		2	14	43	21	4	4	2	4	8		I			
NUMBER	0	8	39	62	36	17	15	10	3	4	I	0	7	39	80	46	28	9	10	12	5	I	0	1	7	21	10	2	2	1	2	4		I		

WIND SPEED 15-19 MPH										I	WIND SPEED GREATER/EQUAL 20 MPH										I	TOTAL	NUMBER	
-----										I	-----										I			
<100										I											I		0	
95-99										I											I		0	
90-94										I											I	2	1	
85-89										I											I	21	10	
80-84										I											I	101	49	
75-79										I											I	216	105	
70-74										I											I	211	103	
65-69										I	2										I	187	91	
60-64										I											I	94	46	
55-59										I	2										I	72	35	
50-54										I											I	60	29	
45-49										I											I	31	15	
40-44										I											I	4	2	
35-39										I											I	2	1	
30-34										I											I		0	
<30										I											I		0	
-----										I	-----										I			
TOTAL										I	2										I	1000		
NUMBER	0	0	2	2	1	0	1	0	0	0	I	0	0	0	0	1	0	0	0	0	0	I		487

(con.)

Table 14 (Con.)

TEMPERATURE - RELATIVE HUMIDITY - WIND SPEED
 PERCENTAGE FREQUENCY OF OCCURRENCE FOR SELECTED COMBINATIONS
 -GIVEN TO TENTHS PERCENT; DECIMAL POINT OMITTED

STATION NUMBER 100417

SPYGLASS LO

1954-1970

MONTH AUG

WIND SPEED 0-4 MPH

I

WIND SPEED 5-9 MPH

I

WIND SPEED 10-14 MPH

RELATIVE HUMIDITY

RELATIVE HUMIDITY

RELATIVE HUMIDITY

TEMP.	1	11	21	31	41	51	61	71	81	91	I	1	11	21	31	41	51	61	71	81	91	I	1	11	21	31	41	51	61	71	81	91	
DEG F	10	20	30	40	50	60	70	80	90	100	I	10	20	30	40	50	60	70	80	90	100	I	10	20	30	40	50	60	70	80	90	100	
<100											I											I											
95-99		2									I											I											
90-94		2	2								I											I											
85-89		11	7								I		2	17								I		2	4	7							
80-84		15	24								I		20	24	4							I				13	2						
75-79		9	35	22	7						I		9	70	22	2						I				9	4						
70-74		4	11	33	11	9					I		4	35	31	13	2					I			9	7							
65-69			4	22	7	11		2			I		4	15	26	22	17			2	2	I				4	9	2	2				
60-64				4	9	13	7	7	2		I			4	17	24	13	7	2	11		I				2	4	4	2				
55-59					7	9	2	2	4		I				4	13	7	2	11		2	I											
50-54					2			4	2	9	I					2		4	4	15	2	I						4	11			2	
45-49							2	2	4	4	I					2				4	4	13	I					4				7	
40-44										2	I										2	I										4	
35-39											I											I											2
30-34											I											I											
<30											I											I											

TOTAL	44	87	85	44	37	9	13	9	15	1	2	50	148	105	76	41	13	24	24	20	1	2	11	44	31	7	13	11		15		
NUMBER	0	20	40	39	20	17	4	6	4	7	1	1	23	68	48	35	19	6	11	11	9	1	1	5	20	14	3	6	5	0	0	7

WIND SPEED 15-19 MPH

I

WIND SPEED GREATER/EQUAL 20 MPH

I

TOTAL NUMBER

<100																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									</
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Finklin, Arnold I.; Fischer, William C. 1987. Climate of the Deception Creek Experimental Forest, northern Idaho. Gen. Tech. Rep. INT-226. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 73 p.

Describes in detail the climate of Deception Creek Experimental Forest and the adjacent area of the Coeur d'Alene National Forest. Data are summarized from year-round climatological stations, fire-weather stations, and other sources.

KEYWORDS: climate, mountain climatology, fire-weather

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

The Intermountain Research Station territory includes Montana, Idaho, Utah, Nevada, and western Wyoming. Eighty-five percent of the lands in the Station area, about 231 million acres, are classified as forest or rangeland. They include grasslands, deserts, shrublands, alpine areas, and forests. They provide fiber for forest industries, minerals and fossil fuels for energy and industrial development, water for domestic and industrial consumption, forage for livestock and wildlife, and recreation opportunities for millions of visitors.

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Bozeman, Montana (in cooperation with Montana State University)

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United States
Department of
Agriculture

Forest Service

Intermountain
Research Station

General Technical
Report INT-227



Gross Characteristics of Lodgepole Pine Trees in North America

Peter Koch



THE AUTHOR

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METRIC CONVERSION FACTORS

English units to metric			Metric units to English		
LENGTH					
1 in	=	25.4 mm (exactly)	1 mm	=	0.0393701 in
1 in	=	2.54 cm (exactly)	1 cm	=	0.393701 in
1 ft	=	0.3048 m (exactly)	1 m	=	3.28084 ft
1 yd	=	0.9144 m (exactly)	1 m	=	1.09361 yd
1 chain (22 yd)	=	20.1168 m (exactly)	1 m	=	0.0497097 chain
1 mi	=	1.60934 km	1 km	=	0.621371 mi
AREA					
1 in ²	=	645.16 mm ² (exactly)	1 mm ²	=	0.0015500 in ²
1 in ²	=	6.4516 cm ² (exactly)	1 cm ²	=	0.15500 in ²
1 ft ²	=	0.0929030 m ²	1 m ²	=	10.7639 in ²
1 yd ²	=	0.836127 m ²	1 m ²	=	1.19599 yd ²
1 mil-acre	=	4.04686 m ²	1 m ²	=	0.247105 mil-acre
1 acre	=	0.404686 ha	1 ha	=	2.47105 acres
1 mi ²	=	2.58999 km ²	1 km ²	=	0.386102 mi ²
VOLUME OR CAPACITY					
1 in ³	=	16,387.064 mm ³	1 mm ³	=	0.000061024 in ³
1 in ³	=	16.38706 cm ³	1 cm ³	=	0.061024 in ³
1 ft ³	=	0.0283168 m ³	1 m ³	=	35.3147 ft ³
1 yd ³	=	0.764555 m ³	1 m ³	=	1.30795 yd ³
1 cunit (100 ft ³ of solid wood)	=	2.83168 m ³	1 m ³	=	0.353147 cunit
1 cord (128 stacked ft ³)	=	3.62456 m ³ (stacked)	1 m ³ (stacked)	=	0.275896 cord
1 bd ft	=	0.002359738 m ³	1 m ³	=	423.7759 bd ft
1 gal (US)	=	3.785412 L	1 L	=	0.264172 gal (US)
MASS OR WEIGHT					
1 grain	=	0.064799 g	1 g	=	15.4324 grains
1 oz	=	28.3495 g	1 g	=	0.0352740 oz
1 lb	=	0.453592 kg	1 kg	=	2.20462 lb
1 ton (short)	=	907.1847 kg	1 kg	=	0.0011023 ton (short)
1 ton (short)	=	0.907185 t	1 t	=	1.10231 tons (short)
1 ton (long)	=	1.01605 t	1 t	=	0.98420 ton (long)
RATIOS					
1 ft ² /acre	=	0.229568 m ² /ha	1 m ² /ha	=	4.35600 ft ² /acre
1 ft ³ /acre	=	0.0699725 m ³ /ha	1 m ³ /ha	=	14.2913 ft ³ /acre
1 cord/acre	=	8.95647 m ³ (stacked)/ha	1 m ³ (stacked)/ha	=	0.111651 cord/acre
1 lb/ft ³	=	16.0185 kg/m ³	1 kg/m ³	=	0.0624280 lb/ft ³
1 ton (short)/acre	=	2.24170 t/ha	1 t/ha	=	0.446090 ton (short)/acre
1 mi/gal (US)	=	0.425143 km/L	1 km/L	=	2.35215 mi/gal (US)

RESEARCH SUMMARY

In the primary study three replications of disease- and insect-free specimens of 76-, 152-, and 228-mm diameter at breast height (d.b.h.) *Pinus contorta* var. *latifolia* Engelm. were collected in low-, medium-, and high-elevation zones (for the latitudinal zone) from nine equally spaced north latitudes (40 through 60 degrees) across 10 degrees of longitude in such a way as to encompass the major range of *latifolia*. Latitudinal and elevational—but not longitudinal—effects on tree characteristics were pronounced.

In a secondary study to examine variations in *murrayana* characteristics, three replications of 76-, 152-, and 228-mm *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm. were collected at medium elevation at four latitudes (37.5, 40, 42.5, and 45 degrees) in California and Oregon at a single longitude per latitude. Also, varietal differences between *latifolia* and *murrayana* were studied in the three latitudes common to the two (40, 42.5, and 45 degrees).

Tree Characteristics, Dimensions, and Cubic Volumes

Because stemwood characteristics of var. *latifolia* are of primary interest to those who process lodgepole pine, averages for a few of the basic characteristics of this variety are shown in the following tabulation; readers are cautioned, however, that values for these characteristics vary significantly with latitude and elevational zone, as well as diameter.

Stemwood characteristic	Diameter at breast height		
	76 mm	152 mm	228 mm
Age at stump height, years	71	91	107
Ring width at stump height, millimeters	0.67	1.01	1.33
Moisture content, percent	----- 99 -----		
Specific gravity, stemwood average	0.43	0.42	0.41
Tree height, meters	9.3	15.6	19.1
Stem length below crown, meters	5.0	8.8	10.9
Stem taper inside bark, below crown, millimeters per meter	6.3	7.8	10.5
Stem taper inside bark, within crown, millimeters per meter	13.1	15.9	18.5

Of all the tree characteristics measured, d.b.h. and stump-root system dimensions were most closely correlated with other tree characteristics. *Latifolia* trees 76-, 152-, and 228-mm d.b.h. averaged 71, 91, and 107 years old, respectively, at stump height of 152 mm. The medium-elevation zone for *latifolia* decreased from about 2,700 m at latitude 40 degrees to about 750 m at 60 degrees. The three diameter classes averaged 9.3, 15.6, and 19.1 m in

height; trees were tallest in latitudes 50 through 55 degrees. Crown ratio was unrelated to d.b.h., and averaged 0.46 for the 243 *latifolia* trees sampled. Stem length below crown averaged 5.0, 8.8, and 10.9 m for the three diameter classes.

Stem crook (sweep) between 10 and 70 percent of tree height was unrelated to d.b.h. and averaged 43 mm. The number of live branches per tree averaged 64, 108, and 133 for trees 76-, 152-, and 228-mm d.b.h.; mean branch diameters were 9, 13, and 19 mm, respectively, with branch angles averaging 85, 79, and 77 degrees. The number of dead branches per tree averaged 57, 100, and 119. Stem diameter at the base of the live crown averaged 52, 100, and 148 mm for the three diameter classes. Only 191 of the 243 trees had cones on the tip 305 mm of the top 25 branches. Southern latitudes had more open-coned trees than northern latitudes. The proportion of complete-tree wood volume comprised of wood from each tree portion averaged as follows: stem to apical tip, 82 percent; live branches, 4 percent; dead branches, 2 percent; and stump-root system to 305 mm radius from stump pith, 12 percent. The bark percentage of gross (wood plus bark) volume of each tree portion averaged as follows (diameter data pooled): stem to apical tip, 11.3 percent; live branches, 37.8 percent; and stump-root system, 14.0 percent.

Varietal differences between *latifolia* and *murrayana* in the latitudes common to the two (40 to 45 degrees) were not major, except that *latifolia* bore significantly more cones than *murrayana*. All of the *murrayana* trees were classified as open-coned, whereas 15 to 50 percent of the *latifolia* trees at these latitudes were classified as closed-coned. Live branch diameter averaged 2 mm less, and branch angle several degrees larger, in *murrayana* trees than in *latifolia*. Live branchbark percentage of gross live branch volume was greater in *murrayana* than in *latifolia*.

Moisture Content of Tree Components

The moisture contents of components of lodgepole pine trees of varieties *latifolia* and *murrayana* are strongly related to latitude and diameter, but less related to elevational zone. Longitudinal zone was studied only for *latifolia*, but no effects were discernible.

Differences between the moisture contents of tree components of *latifolia* and *murrayana* were minor—most related to bark moisture contents; in latitudes 40, 42.5, and 45 degrees *latifolia* bark moisture content tended to be positively correlated with latitude, whereas bark moisture of *murrayana* was negatively correlated with latitude.

Throughout the full range of latitude (40 to 60 degrees) in which *latifolia* moisture contents were studied, however, there was a pronounced decrease in *latifolia* tree-component moisture content from south to north. Maximum moisture contents usually occurred at latitude 42.5 or 45 degrees, and minimums were observed between 52.5 and 60 degrees. For example, stemwood moisture content (diameter data pooled) averaged 124 percent at 42.5 degrees and only 83 percent at 60 degrees. Similarly, stembark moisture content averaged 131 percent at 45 degrees but only 80 percent at 52.5 degrees.

Moisture contents of the following components were inversely correlated with d.b.h. (that is, moisture contents were higher in trees 76 mm in d.b.h. than in trees of larger diameter): complete trees (with or without foliage), foliage, stembark, heartwood, and wood and bark of the stump-root system. Sapwood, however, had higher moisture content in trees of large diameter than in those of small diameter.

The moisture content of both wood and bark increased sharply from stump height to upper stem; the increase was greater in bark (72 to 165 percent) than in wood (90 to 130 percent).

Moisture contents of tree components were most closely and most frequently correlated with specific gravity of wood and bark of components, heartwood percentage of stemwood volume, sapwood thickness at stump height, and with crown ratio.

Tree average moisture contents (all *latifolia* data pooled) for tree components were generally in the range from 90 to 110 percent of oven-dry weight, with exceptions as follows: cones (26 percent), dead branchwood (18 percent), sapwood (119 percent), heartwood (43 percent), and bark of lateral roots (121 percent).

Significant variations related to latitude, d.b.h., elevational zone, and height in tree are so large, however, that variety-wide generalizations about average moisture contents of tree components should be made with caution.

Stem Taper

Stems of large-diameter *latifolia* and *murrayana* trees flared more in the butt section than those of smaller diameter—both inside and outside bark. Below-crown average stemwood taper averaged 8.2 mm/m (3.6 standard deviation) for *latifolia* and 9.5 mm/m (4.7) for *murrayana*; in both, this taper was positively correlated with d.b.h. *Latifolia* trees 228 mm in d.b.h. from high elevational zones had more below-crown stemwood taper than those from medium or low zones. *Latifolia* trees in Canadian latitudes had less below-crown stemwood taper than those in United States latitudes. Least below-crown taper was found in small-diameter, slow-grown trees with little foliage, small branches, narrow crowns, thin bark, and small central stump-root systems.

Within-crown stemwood taper was also positively correlated with d.b.h., but was much greater than below-crown taper; it averaged 15.8 mm/m (4.1) for *latifolia* and 15.7 (4.8) for *murrayana*. Trees from high-elevation zones had more within-crown stemwood taper than those from low and medium zones. Within-crown stemwood taper in *latifolia* averaged least in the middle latitudes (45 to 50 degrees). For all *latifolia* it was least in small trees with small branches, narrow crowns with few cones, high crown ratios, low heartwood content, and small central stump-root systems.

For both varieties stem diameter inside bark at the base of the live crown was proportional to d.b.h.; it averaged 52 mm (11), 100 mm (18), and 148 mm (23) for *latifolia* and 58 mm (12), 108 mm (17), and 169 mm (21) for *murrayana* in trees 76, 152, and 228 mm in d.b.h. Stem diameter inside bark at the base of the live crown was least in small, thin-barked trees with little heartwood, small stump-root

systems, and short, narrow crowns with small branches. In *latifolia* trees, stem diameter at the base of the live crown tended to be larger in southern latitudes than in northern.

Stemwood volume within crown, as a percentage of total stemwood volume, averaged 16.0 percent (12.1) for *latifolia* and 26.5 percent (13.8) for *murrayana*. This proportion was unrelated to elevational zone or d.b.h. *Latifolia* in Canadian latitudes had only 12.2 percent within-crown stemwood, whereas trees of this variety in the United States averaged 20.8 percent. Within-crown stemwood had the least proportion of total stemwood volume in tall but short-crowned older trees having low moisture content, high heartwood content, high specific gravity of bark and sapwood, and thin stembark.

Longitudinal effects on taper characteristics were absent or minor.

Specific Gravities and Weights of Tree Components

The most important finding of this research is that stemwood specific gravity of *latifolia* trees 76, 152, and 228 mm in d.b.h.—in a spectrum of ages—decreased with increasing d.b.h., and increased with increasing latitude. With diameter, latitudinal, and elevational data pooled, *latifolia* stemwood specific gravity averaged 0.418 (sapwood averaged 0.414 and heartwood 0.434) based on unextracted oven-dry weight and green volume. As noted above, *latifolia* stemwood specific gravity was negatively correlated with d.b.h., averaging 0.427, 0.419, and 0.407 for trees 76, 152, and 228 mm in d.b.h. Trees in the three diameter classes averaged 71, 91, and 107 years old, respectively, with growth-ring width at 152 mm stump height averaging 0.67, 1.01, and 1.33 mm.

Stemwood specific gravity diminished with increasing height in tree up to the base of the live crown, above which it remained constant or increased slightly at values between 0.39 and 0.40. At all percentages of heights in the stems, small-diameter trees had higher stemwood specific gravity than large trees. For all diameters, stemwood specific gravity could be closely estimated from stemwood specific gravity at 20 percent of tree height. Stemwood specific gravity was unrelated to elevational zone within latitudinal sampling zone, but was positively correlated with latitude, averaging minimum (0.390) at 42.5 degrees and maximum (0.435) at 55 degrees. This specific gravity trend was inverse to stemwood moisture content trend with latitude, and aligned with the trend of heartwood percent of stemwood weight.

Wood of *latifolia* live branches had higher average specific gravity (0.487) than that of the stump-root system (0.469) or stem (0.418). Specific gravity of bark of live branches, stump-root system, and stem averaged 0.411, 0.415, and 0.369, respectively.

Complete *latifolia* trees 76, 152, and 228 mm in d.b.h. had average oven-dry weights of 28, 170, and 440 kg, including foliage and stump-root systems to a lateral-root radius of 305 mm from stump pith. Trees from high elevational zones weighed less than those from low. With diameter and elevational data pooled, trees weighed least in the three southernmost latitudes (40 through 45 degrees) and most in latitudes 47.5 through 55 degrees.

Latifolia tree component proportions varied significantly with d.b.h., latitude, and elevation; but with all data pooled, component weight percentages (ovendry) averaged 6.8, 1.0, 5.9, 2.0, 72.8, and 11.5 percent for technical foliage, cones, live branches, dead branches, stem, and stump-root system. Small trees had a greater proportion of foliage and stump-root system, and a lesser proportion of cones, live branches, and stem weight than large trees.

The weight of *latifolia* green wood plus bark of the three major tree components required to provide 1 m³ of bark-free wood was greater for small trees than large, and varied with latitude and elevation. With all data pooled, average requirements for foliage-free branches, stem (152 mm stump height to apical tip), and stump-root system were 1,448, 920, and 1,046 kg, respectively.

Bark ovendry-weight proportions of tree components were greater in small trees than large, and varied with latitude and elevational zone. With all *latifolia* data pooled, however, averages were 11.6, 10.1, 33.8, and 12.5 percent for complete foliage-free tree, stem, live branches, and stump-root system, respectively.

Variations related to longitudinal zones across latitudinal sampling zones were minor, except that individual *latifolia* cones from trees on the east end of sampling zones weighed more than those on trees from the west end.

At the three latitudes the two varieties had in common (40, 42.5, and 45 degrees), *murrayana* had higher specific gravity for most tree components than *latifolia*; for example, stemwood of *murrayana* averaged 0.451 vs. 0.401 for *latifolia*, and specific gravity of bark of complete trees averaged 0.387 for *murrayana* vs. 0.363 for *latifolia* (basis of ovendry weight and green volume).

Latifolia had more weight of foliage per tree, and a higher foliage-weight proportion (7.3 percent vs. 5.3 percent, ovendry basis).

With diameter data pooled, 1,025 kg of *murrayana* stems (wood plus bark, green) is required to yield 1 m³ of bark-free wood, whereas only 926 kg of *latifolia* will yield this volume of wood.

Distribution, Moisture Content, Weight, and Specific Gravity of Heartwood and Sapwood

In *latifolia* the age of the lowest tree disk where heartwood did not occur averaged 21, 11, and 10 years in trees 76, 152, and 228 mm in d.b.h.; this age was also negatively correlated with latitude. The height of this lowest heartwood-free disk averaged 76, 89, and 93 percent in trees of the three diameters, and was positively correlated with latitude.

The height (above a stump height of 152 mm) in *latifolia* at which maximum heartwood diameter occurred averaged 0.80, 0.53, and 0.44 m for trees 76, 152, and 228 mm in d.b.h.; this height was also negatively correlated with latitude. Heartwood percentage of stem diameter at height of maximum heartwood diameter was positively correlated with latitude, and averaged 48, 54, and 59 percent for trees of the three diameter classes.

In *latifolia*, minimum sapwood thickness where heartwood was present averaged 16, 24, and 29 mm for trees

76, 152, and 228 mm in d.b.h.; trees in northern latitudes and middle to upper elevational zones (within latitudinal zones) had thinnest sapwood. This minimum sapwood thickness occurred at 51, 60, and 70 percent of height in trees of the three diameter classes; the percentage of height was positively correlated with latitude. Sapwood thickness was maximum near ground level, diminished rapidly up to about 10 percent of tree height, then remained more or less constant to about 70 percent of tree height, and finally diminished with approach to the apical tip. Sapwood was thinnest in northern latitudes.

Heartwood volume as a percentage of entire stemwood volume in *latifolia* averaged 22, 28, and 34 percent in trees 76, 152, and 228 mm in d.b.h.; heartwood volume percentages were positively correlated with latitude.

Sapwood moisture content in *latifolia* averaged 119 percent, with moisture contents of 110, 122, and 126 percent in trees 76, 152, and 228 mm in d.b.h.; it was negatively correlated with latitude. Sapwood moisture content was minimum in the lowest 10 percent of the stems (110 percent), increased more or less linearly to a maximum (136 percent) at about 80 percent of tree height, and then diminished slightly toward the apical tip.

Heartwood moisture content in *latifolia* averaged 43 percent, with moisture contents of 47, 42, and 41 percent in trees 76, 152, and 228 mm in d.b.h. Heartwood moisture content averaged minimum (42 percent) at stump height of 152 mm, and increased curvilinearly to a maximum (52 percent) at 90 percent of tree height.

Heartwood percentage of ovendry weight of entire *latifolia* stemwood averaged 23, 29, and 35 percent for trees 76, 152, and 228 mm in d.b.h.; these percentages were positively correlated with latitude.

Specific gravity of sapwood in entire stems (based on green volume and unextracted ovendry weight) averaged 0.414, and was maximum at middle latitudes; it was 0.423, 0.415, and 0.405 in trees 76, 152, and 228 mm in d.b.h. Sapwood specific gravity averaged 0.449 at stump height, decreased to a minimum of 0.387 at 70 percent of tree height, and then increased to 0.399 at 90 percent of tree height.

Specific gravity of heartwood of entire *latifolia* stemwood averaged 0.434; it was 0.459, 0.430, and 0.412 in trees 76, 152, and 228 mm in d.b.h. With diameter data pooled, heartwood had average specific gravity of 0.482 at stump height of 152 mm, decreased sharply to a minimum of 0.412 at 30 percent of tree height, and then increased to a near maximum (0.478) at 90 percent.

In the three latitudinal sampling zones common to the two varieties (40, 42.5, and 45 degrees), some significant differences were observed between *latifolia* and *murrayana* in heartwood and sapwood characteristics. In *latifolia* maximum heartwood diameter occurred at an average of 8.5 percent of tree height (1.01 m above stump top); it averaged lower in *murrayana* (6.3 percent and 0.81 m). Specific gravity of entire sapwood averaged significantly higher in *murrayana* (0.444) than in *latifolia* (0.397); at all heights in trees, *murrayana* had greater sapwood specific gravity than *latifolia*. Specific gravity of heartwood also averaged significantly higher in *murrayana* (0.500) than in *latifolia* (0.427); this relationship applied to all latitudes, diameters, and heights in trees.

Gross Characteristics of Lodgepole Pine Trees in North America

Peter Koch

CHAPTER 1: TREE CHARACTERISTICS, DIMENSIONS, AND CUBIC VOLUMES

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1-1 THE LODGEPOLE PINE RESOURCE IN NORTH AMERICA

Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) occupies about 5.25 million ha of commercial forest land in the United States (containing 748 million m³ of lodgepole growing stock and over 71 billion bd ft of lodgepole timber, mostly in Montana, Idaho, Wyoming, Colorado, and Oregon), and is the fourth most extensive timber type west of the Mississippi River. On these 5.25 million ha, a significant proportion of the trees are dead, having been killed by insects. In the Northern Region alone, a 1979 survey reported 540,862 ha severely infested with mountain pine beetle. The most recent survey data for Idaho indicate that insects and disease have killed about 1 percent of the lodgepole pine trees. Canada has a greater acreage of lodgepole pine forest type (20 million ha, comprising 22 percent of the total forest land in western Canada) than the United States.

Most of the North American lodgepole pine resource is of the variety *latifolia* (*Pinus contorta* var. *latifolia* Engelm.) centered along the Rocky Mountains from 40 to 60 degrees north latitude, with Sierra lodgepole pine (*Pinus contorta* var. *murrayana* [Grev. & Balf.] Engelm.), and shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) comprising significantly lesser volumes on Sierra and coastal areas (fig. 1-1). A fourth variety (*bolanderi* [Parl.] Vasey) is a shrub confined to Mendocino County, CA.

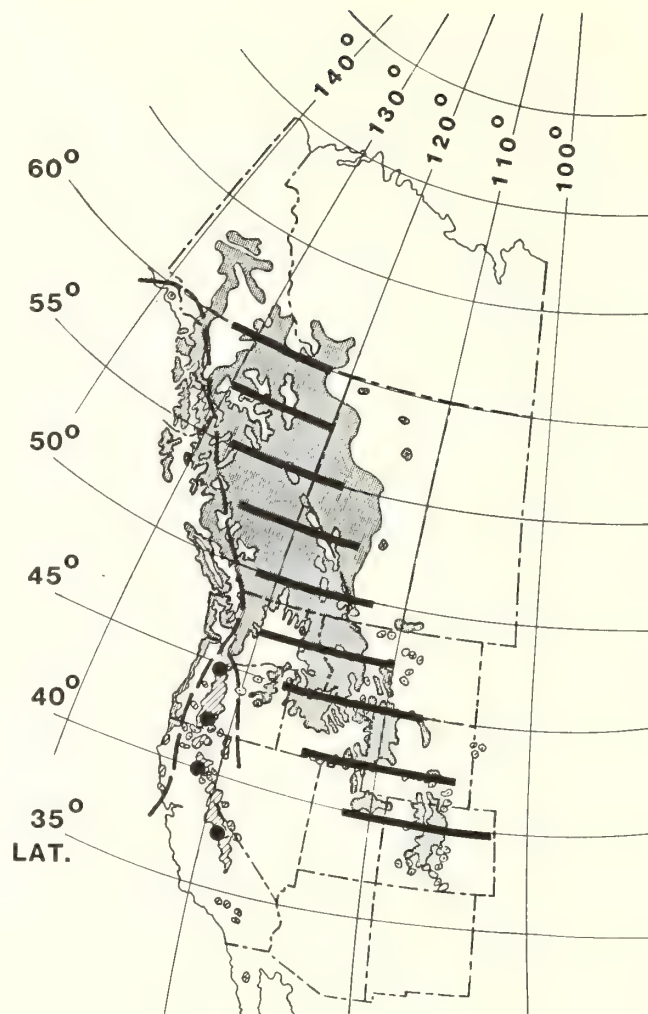


Figure 1-1—Sampling zones superimposed on Little's (1971) range map of lodgepole pine in North America. Variety *latifolia* is mapped to the right of the dashed lines, *murrayana* between them, and *contorta* to the left of them. Variety *contorta* was not studied because of its small potential for commercial use.

In both Canada and the United States, much of the lodgepole pine resource is in older (60 to 200 years), virtually stagnated stands in which growth rate is very low and mortality very high (fig. 1-2). Typically, trees are small in diameter. Slightly more than one-third of the volume (ovendry weight basis) is in trees less than 175 mm in diameter measured at breast height outside bark (Van Hooser and Chojnacky 1983); such a diameter might be considered the lower limit for lumber manufacture.

Silvicultural treatments (thinning or removal and regeneration to managed stand with controlled stocking) are so expensive, and stumpage revenue so little, much of the acreage has received no treatment to accelerate growth and slow mortality.

1-2 GENERAL STUDY PLAN AND OBJECTIVES

This General Technical Report, presenting gross characteristics of lodgepole pine trees in North America, comprises five chapters, as follows:

- Chapter 1: Tree Characteristics, Dimensions, and Cubic Volumes
- Chapter 2: Moisture Content of Tree Components
- Chapter 3: Stem Taper
- Chapter 4: Specific Gravities and Weights of Tree Components
- Chapter 5: Distribution, Moisture Content, Weight, and Specific Gravity of Heartwood and Sapwood.

These five chapters are part of the initial output of a decade-long (1983-93) research program intended to improve utilization of lodgepole pine forests of the 21st century in North America. Details of this program can be found in Koch (1985).

Further reports—beyond this initial five-chapter General Technical Report on gross tree characteristics—will provide data on anatomical, chemical, mechanical, and additional physical characterization of tree components as industrial raw materials; most should be complete by 1990.

The entire characterization effort is confined to varieties *latifolia* and *murrayana*, with emphasis on the former. Tree data will primarily be correlated with diameter at breast height outside bark (d.b.h.), and with elevational, latitudinal, and longitudinal zones. Also, within-tree variation in properties with height and radial position will be determined. Properties of variety *latifolia* and those of *murrayana* will be compared for trees in latitudinal zones common to both varieties.

The primary objective during tree collection was to obtain disease- and insect-free specimens of 76-, 152-, and



Figure 1-2—Natural unthinned lodgepole pine stand (var. *latifolia*) in low-elevation zone (716 m) at 55 degrees latitude 12 km north of Fort St. James, BC. The tree sampled here, next to the stadia rod, measured 155 mm d.b.h., 19.1 m high from stump top to apical tip, and was 163 years old.

228-mm lodgepole pine (var. *latifolia*) at low, medium, and high elevations from nine equally spaced north latitudinal zones (40 to 60 degrees) across 10 degrees of longitude, in such a way as to encompass the major range of this variety (fig. 1-1).

A secondary objective was to sample these same three diameter classes of var. *murrayana* at midelevation at four north latitudes (37.5, 40, 42.5, and 45 degrees) in California and southern Oregon at a single longitude per latitude (fig. 1-1).

The trees of both varieties were sampled in such a way that between-variety comparisons could be made for mid-elevation trees from latitudes 40, 42.5, and 45 degrees. The collection totaled 243 *latifolia* trees and 36 *murrayana* trees.

Chapter 1 presents results of analyses of gross tree characteristics, dimensions, and cubic volumes.

1-3 LIMITATIONS OF THE STUDY

A work of this scope, broadly describing trees of a species with great latitudinal, longitudinal, and elevational range, cannot meet the needs of readers of all disciplines. Recognizing this reality, the work was written principally for use by industrialists, scientists, process engineers, and students who need a description of gross species characteristics and some appreciation of their variations within North America.

Because the sampling plan calls for a specimen collection stratified by d.b.h., latitude, and elevational zone—without sampling intensity adjusted for volume distribution within these stratifications—it does not permit computation of species-average values valid rangewide.

Moreover, the sampling plan does not permit evaluation of effects of site quality, age, and stand density—even though it is well known that these three parameters significantly affect many, perhaps most, of the characteristics evaluated. This shortcoming in experimental design was thoroughly discussed before study initiation.

Because resources available for this study of lodgepole pine as an industrial raw material were not only finite, but modest, the study objectives were limited to determination of broad material characteristics variations related to tree d.b.h. and spatial location (latitude, longitude, and elevational zone). The study was not designed to deal with the very complex relationships involving site quality, tree age, or stand density; as a result, the sampling plan does not permit such analyses.

The elevational range of lodgepole pine (*latifolia*) is considerably greater in southern latitudes than in northern (fig. 1-3); and therefore site quality and stand densities probably vary less in northern than in southern latitudes.

1-4 CANADIAN COOPERATION

The Canadian Forestry Service, working through the University of British Columbia, was able to accomplish collection of the 135 trees along the five latitudes in that nation during the summers of 1983 and 1984; the collection was made under the direction of Dr. Robert Kennedy, Dean of Faculty of Forestry, University of British Columbia. This substantial contribution to the overall effort is appreciatively acknowledged. Extending the collection from near the southern limit to near the northern limit of the species range greatly enhanced its value.

1-5 PAST WORK ON CHARACTERIZATION

Simultaneously with our characterization effort, an exhaustive review of the world literature on lodgepole pine has been accomplished. It is evident from the approximately 4,000 publications comprising this body of literature on lodgepole pine, that research efforts have been largely

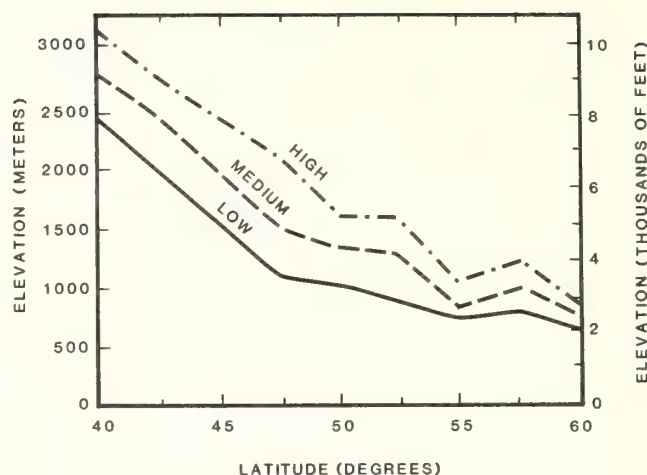


Figure 1-3—Elevational trends in the three zones (low, medium, and high) where lodgepole pine (var. *latifolia*) was sampled along nine latitudes. Each plotted point is the average for nine trees; that is, three diameters by three replications.

devoted to provenance trials, regeneration technology, silviculture, growth and yield, physiology and ecology, watershed and wildlife management, fire management, and insect and disease problems—particularly problems related to the mountain pine bark beetle. Probably less than 3 percent of the literature deals directly with utilization of the species.

There are essentially no data in the literature that provide an integrated overview of the anatomical, physical, chemical, and mechanical properties of varieties *latifolia* and *murrayana* related to latitude, elevational zone, diameter class, and longitudinal zone spanning the major range of these trees in North America. Because of this lack of characterization overview, literature related to the first chapter—which deals with a very large number of diverse characteristics—is not abstracted. Instead, table 1-1 lists references peripherally pertinent to introducing all five chapters (for example, those references concerned with species, botanical descriptions, and keys) and those regionally pertinent to the subject matter of chapter 1. This tabulation should be useful to readers wishing to study listed topics in greater depth.

In chapters 2 through 5, which individually deal with a narrower range of topics, a thorough summarization of the pertinent world literature is provided.

Table 1-1—References pertinent on a regional and local basis to the subject matter of this paper, and to subjects peripherally pertinent to the series of papers

Subject	References
Bark thickness	(Citations marked with an * relate to attack by mountain pine beetle or other insect) Amman (1969*, 1972*), Amman and Pace (1976*), Berryman (1976*, 1978*), Blyth (1955), Cabrera (1978), Cerezke (1973*), Cole (D.M. 1973*), Cole (D.M.) and Jensen (1980), Cole (W.E. 1973*), Cole (W.E.) and Amman (1980*), Cole (W.E.) and Cahill (1976*), Faurot (1977), Hawksworth and others (1983*), Kozak and Yang (1981), Lange (1971), Myers (1964a), Parker (1950), Shrimpton and Thomson (1983*), Smith and Kozak (1971), Smithers (1961), Spada (1960), Spalt and Reifsnnyder (1962)
Bark volume	Drake (1983), Faurot (1977), Hakkila and Panhelainen (1970), Kozak and Yang (1981), Snell and Max (1982)
Branch characteristics	Franklin (1964), Franklin and Callaham (1970)
Branch volume	Faurot (1977)
Cone serotiny	Armit (1964,1966), Bates (1917,1930), Brown (1975), Cooper and others (1959), Critchfield (1980), Crossley (1955,1956a,1956b), Hartl (1979), Hellum and Barker (1980,1981), Hellum and Pelchat (1979), Kamra (1982), Knapp and Anderson (1980), Kovalchik and Blake (1972), Linhart (1978), Lotan (1963, 1964,1967,1968, 1970,1975a,1975b,1976), Lotan and Jensen (1970), Lotan and Perry (1983), Macaulay (1976), Moore (1981b), Mowat (1960), Muir (1982), Muir and Lotan [in press], Perry and Lotan (1979), Sutherland and others (1982), Tackle (1959), Teich (1970), Tower (1909)
Cone yield	Lotan (1963,1975a,1975b), Lotan and Jensen (1970), Moore (1981a,1981b), Smithers (1961), Thompson (1978)
Crown dimensions	Alexander (1974), Alexander and others (1967), Bonnor (1964), Brown (1976,1978), Chapman and others (1982), Cole (1983), Cole and Jensen (1983), Dahms (1966, 1971a), Eis and others (1982), Fahnestock (1960), Gary (1974,1976,1978), Kimes and others (1979), Matthews (1963), Moeur (1981), Mogren (1967), Muller (1971), Smith and Bailey (1964), Smithers (1961), Wellner and Lowery (1967)
Crown ratio	Brown (1978), Cole and Jensen (1983)
Elevational effects	Amman (1973), Amman and others (1973,1977), Bannan (1964), Benecke and Morris (1978), Clausen (1965), Cole (D.M.) and Stage (1972), Cole (W.E.1973), Cole (W.E.) and Amman (1980), Cunningham and Roberts (1970), Forestry Research West (1983), Hagner (1980a,1980b), Hawksworth (1956), Hobbs and Partridge (1979), Illingworth (1971), Krajina (1970), Larson (1978), Lindgren and others (1976), Lotan and Perry (1983), Moore (1981a), Neustein (1966),

Table 1-1—Con.

Subject	References
	Rehfeldt (1980,1983), Rehfeldt and Wykoff (1981), Safranyik (1978), Scott (1970), Shepperd and Alexander (1983), Smithers (1961)
Geographic variation	Biro (1978), Critchfield (1957), Dietrichson (1970), Forrest (1977a,1977b,1979,1981), Hagner (1980a,1980b), Henderson and Petty (1972), Illingworth (1969,1971,1976), Jeffers and Black (1963), Knowles (1980), Knowles and Grant [in press], Maschning (1971), Mirov (1954a,1954b), Moore (1981a,1981b), Mowat (1960), Newman and Jancey (1981), Nilsson (1981), Nyland (1980), Perry (1975), Perry and Lotan (1978), Smith (R.H.1983), Wheeler and Guries (1982a,1982b), Yeh and Layton (1979), Ying and others (1985)
Height-diameter data	Cole (D.M.) and Edminster (1985), Myers (1966)
Latitudinal effects	Alden and Zasada (1983), Amman and others (1977), Christie and Lines (1979), Hagner (1980a,1980b), Illingworth (1971), Jonsson and others (1981), Krajina (1970), Lindgren and others (1976), Moore (1981a,1981b), Safranyik (1978), Taylor and others (1982)
Root form (excluding seedlings)	Berndt and Gibbons (1958), Bishop (1962), Boggie (1972), Gail and Long (1935), Horton (1958), Nielsen (1982), Pfeifer (1982), Smith (J.H.G. 1964), Smithers (1961), van Eerden and Kinghorn (1978)
Species descriptions: general; mostly of var. <i>latifolia</i>	Anderson and Tiedemann (1970), Barrett and others (1983), Betts (1945), Davies (1980), Dietrichson (1970), Edwards (1954,1955), Fosberg (1959), Guernsey and Dobie (1966), Hosie (1973), Illingworth (1976), Kotok (1971), Laing (1955), La Roi and Hnatiuk (1980), Loope (1971), Lotan and Alexander (1973), Lotan and Critchfield [in press], Lotan and Perry (1983), MacDonald and Wood (1957), McDougal (1975), Ministry of Technology (1965), Mirov (1954a,1954b), Moore (1981b), Moss (1955), Nyland (1980), O'Driscoll (1978,1980), Paul (1962), Pfister and Daubenmire (1975), Pfister and others (1977), Polge (1963), Reid, Collins Nurseries, Ltd. (1983), Roche (1966), Satterlund (1975), Schmidt (1981), Smithers (1961), Tackle (1959), Trappe and Harris (1958), U.S. Department of Agriculture, Forest Service (1973), van den Driessche (1956-1957), Wellner (1975), Wheeler and Critchfield (1985), Wheeler and Guries (1982a,1982b), Wikstrom (1957)
Species descriptions: <i>bolanderi</i> literature	Hanan (1963), Jenny and others (1969), McMillan (1956,1964), Westman (1975,1978), Westman and Whittaker (1975), Wheeler and Critchfield (1985)
Species descriptions: shore pine literature	Critchfield (1965), Davidsonia (1979), Davies (1980), Dunsworth and others (1982), Kumler (1969), Moss (1971), Peattie (1952), Pederick (1980), Peterson and Harvey (1976), Roche (1963), Smith (R.B. 1971), Swan (H.S.D.

(con.)

Table 1-1—Con.

Subject	References
	1972), Thiers (1973), U.S. Department of Agriculture (1964), van den Driessche (1956-1957), Wass (1976), Wheeler and Critchfield (1985)
Species descriptions: Sierra lodge-pole literature	Agee (1983), Clausen (1965), Dykstra (1974), Griffin and Critchfield (1972), Gunther (1929), Harris (1973), Laing (1955), Little (1966), Manning and Hemmingson (1975), McMillan (1964), Righter and Stockwell (1949), Shirling (1946), Smith (F.W. 1981), Stock and others (1978), Struble (1967,1968), U.S. Department of Agriculture (1964), Went (1973), Wheeler and Critchfield (1985), Wheeler and Guries (1982b)
Species descriptions: Keys to species	Bagnell (1975; pollen key), Barton (1975; extractives key), Bates (1925; seedling key), Gilbertson and others (1961; root key), Hansen and Cushing (1973; pollen key), Kellogg and others (1982; wood anatomy key), Laing (1955; botanical key), Longyear (1908; botanical key), Mack (1971; pollen key), Mayer and Fox (1981; LANDSAT digital classification key), Swan (E.P.) (1966; chemical key to wood), Weir and Thurston (1977; pollen key)
Species descriptions: Keys to varieties	Fosberg (1959; botanical key)
Species descriptions: Keys to geographic origin	Forrest (1977a,1977b,1979,1981; chemical key), McMullan and Colangeli (1982; chemical key)
Stem crook (sweep)	Dobie and Middleton (1980), Fitzsimons (1982), Hornibrook (1950), Kotok (1967), Lines and Booth (1972), Lines and others (1971), Malcolm (1968), Moss (1971), Pfeifer (1982), Schroeder and Phillips (1984), Sterba (1980)
Stem volume and volume tables	Alemdag (1973,1976), Allen and others (1976), Berry (1981), Blyth (1955), Bonnor (1966), British Columbia Forest Service (1936), Chapman and others (1982), Cole (D.M. 1971,1979,1983), Cole (D.M.) and Edminster (1985), Dahms (1964,1971b,1975), Dominion Forest Service (1944), Duff (1956,1966), Duffy and Meyer (1962), Edminster (1978), Eis and others (1982), Eriksson (1973), Faurot (1977), Hamilton and Christie (1971), Hanzlik (1916), Heger (1965), Honer (1967), Hornibrook (1948), Jeffers and Spragg (1966), Johnson (1952,1955), Johnstone (1975,1976), MacLean and Berger (1976), Massie and others (1983), Moessner (1957), Myers (1964b,1967,1969), Oregon State Board of Forestry (n.d.), Plank and Cahill (1984), Quintus (1951), Smith (J.H.G.) and Ker (1957), Smithers (1961), Upson (1914), Ziegler (1907)
Stump volume	Raile (1982)
Root volume (cubic)	No literature found

1-6 GENERAL STUDY PROCEDURES

Locating and Selecting the 243 *Latifolia* Trees

The sample area spanned from 40 to 60 degrees (inclusive) at 2.5-degree intervals; the width of the sample area was 10 degrees of longitude, with sample area shifting 2.5 degrees west for each 2.5 degrees shift north in latitude (fig. 1-1). Sample band width was 0.5 degree of latitude on each side of the nominal latitude line; that is, each latitude band was 1 degree deep in the north-south direction (60 nautical miles), and 10 degrees of longitude wide in the east-west direction.

Within each of these nine latitudinal sampling bands, natural unthinned stands were identified, with the following constraints: adjacent to road traversable by pickup truck; within boundaries of National or Provincial Forests; and containing some more-or-less level benches or flats.

It was found that at least nine such stands could be identified within each sampling band. The identified stands were ranked by elevation, and then the three highest, the three most intermediate, and the three lowest were selected for sampling. These elevational zones were highest in the south and lowest in the north; elevational zone width was broadest at midlatitude (fig. 1-3).

On a bench or flat typical of each of these selected stands, single trees 76, 152, and 228 mm in d.b.h. and free of insects and diseases were taken that in the collector's view typified within-stand trees of these diameters on that bench or flat. Thus, 27 *latifolia* trees were taken from each of the nine latitudes—3 diameters × 3 elevations × 3 replications, for a total of 243 trees.

It is important to note that this sampling scheme resulted in selection of 76-, 152-, and 228-mm trees that were of approximately the same age, because most of the stands were of fire origin. Thus, most of the small-diameter trees were suppressed, while the larger trees were the fast growers.

Locating and Selecting the 36 *Murrayana* Trees

The sample areas extended from 37.5 to 45 degrees latitude at 2.5-degree intervals; that is, trees were sampled at 37.5, 40, 42.5, and 45 degrees—but only at one longitude per latitude (fig. 1-1).

The same three constraints on location applied to *latifolia* also applied to *murrayana*, but *murrayana* was sampled only from midelevation, as follows:

Latitude	Elevation	
	Meters	Feet
Degrees		
37.5	2,402	7,880
40	1,676	5,499
42.5	2,006	6,581
45	1,148	3,766

Thus, nine *murrayana* trees were taken from each of the four latitudes—3 diameters × 1 elevation × 3 replications, for a total of 36 trees.

Field and Laboratory Work

General Field Procedure—All fieldwork was completed during the summer months of 1983 and 1984. After selection of each tree a photograph was taken of it (with its identifying code number), a note made regarding the soil type, and a record made of the following data: latitude, longitude, elevation, diameter at breast height, and date. The tree was trenched as though the lateral roots were severed by a tube 0.9 m in diameter centered on the tree pith. The tree was uprooted and the root brushed free of dirt; an effort was made to extract whatever taproot there was to a diameter of 1 inch. Total tree height was measured from the top of a 152-mm-high stump to the apical tip, and also to a 25.4-mm stem diameter measured outside bark.

Length of stump-root system was measured from stump top to the bottom of whatever taproot there was. Length and width of the live crown were measured. The lateral root system was pruned back to a 305-mm radius, and the complete tree with attached stump-root system and intact foliage weighed.

Following all the field procedures described in subsequent paragraphs, selected tree parts were trucked to the Forestry Sciences Laboratory of the Intermountain Research Station in Missoula, MT, for prompt (<3 weeks) analysis.



Figure 1-4—Variation in root form of trees measuring 228 mm (left), 152 mm (center), and 76 mm (right) in d.b.h. sampled at latitude 47.5 degrees from three elevational zones. The scale marks on the chalkboards indicate 152 mm.

Central Stump-Root System Procedure—In the field, the stump-root system was severed at 152 mm stump height, weighed, and sealed in a polyethylene bag. At the Missoula laboratory, the root system was further cleaned and all roots smaller than 6 mm in diameter were trimmed; the stump-root system was then weighed and photographed. Typically, the stump-root systems were characterized by a stout taproot, with length positively correlated ($r = 0.625$) with tree d.b.h.; great variation in root form was observed (fig. 1-4). The system was then segmented into three portions (stump top to root collar, lateral roots, and central root mass including the root collar and taproot), and each portion weighed while green and the volume measured by water immersion. Bark thickness of each portion was measured. The bark was then removed from each portion, the bark-free weight and volume recorded, and the bark of each portion oven-dried and weighed. Wood from each portion of the stump root was sampled and oven-dried to determine moisture content. All three portions were retained in specimen storage.

Cones Procedure—In the field, all cones on the first lineal 305 mm of the top 25 live branches (excluding the apical tip) were counted, clipped, and the number of closed cones in this sample recorded. A subsample of a few cones was sealed in polyethylene for later determination of moisture content. The remainder of the clipped cones were bagged in muslin (with additions from the first 305 mm of live branches 26 through 50, if necessary to obtain a sufficient supply) for analyses of anatomy and heat of combustion. In the laboratory the green weight and moisture content of the cones were determined, the muslin-bagged cones air dried and stored, and by Lotan and Jensen's (1970) formula the total number of cones on the tree calculated.

Dead Branches Procedure—In the field, the number of dead branches was counted; after the complete tree was weighed, all dead branches were clipped entire (flush with the stem) and weighed. From the total population of dead branches, ten 152-mm-long lengths from branch midlength were randomly sampled and sealed in a polyethylene bag for laboratory determination of moisture content and specific gravity.

Foliage Procedure—In the field, foliage from the four live branch whorls nearest 60, 70, 80, and 90 percent stem height was clipped and put in a polyethylene bag for laboratory determination of moisture content; additional foliage from the same branches was collected for air drying and laboratory determination of properties. This foliage, together with all of the other technical foliage (all needles and needle-bearing twigs up to 6 mm diameter outside bark) on the tree were weighed in aggregate.

Live Branches Procedure—On the three branches nearest the 60, 70, 80, and 90 percent stem level (12 branches in all per tree) each branch diameter was measured 50 mm from the stem, outside bark; also, branch angle was measured at point of entry to the stem (ascending branches have angles less than 90 degrees, while drooping branches have angles more than 90 degrees). From each of these branches a 203-mm length was taken at midlength and bagged in polyethylene for laboratory determination of moisture content and specific gravity.

From adjacent branches similar lengths were taken for air drying and laboratory determination of other properties. In the field, these subsamples plus the branch ends and butts and all of the other foliage-free branches on the tree were weighed to get an aggregate live-branch weight.

In the laboratory, the moisture-content lengths were weighed green, and their volume measured by water immersion. The average thickness of the bark on each length was recorded, the bark removed, and the weight and volume of the bark-free length recorded. The oven-dry weight of each bark-free length was then recorded, and also the oven-dry weight of the bark from each length.

Stem Procedure—In the field, the stem was shorn of branches so that it was complete from 152-mm-high stump to apical tip. By stretching a taut string between the 10- and 70-percent stem levels, the maximum crook was measured and recorded together with the stem level at which it occurred.

From the 0, 10, 20, 30, 40, 50, 60, 70, 80, 90 percent, and apical-tip level of the stem, a pair of disks was removed—one 50 mm thick and bagged in polyethylene for laboratory determination of moisture content and specific gravity, the other 75 mm thick and air dried for laboratory determination of additional properties.

Also transported from field to laboratory were two stem sections with bark in place—the first between stem levels 10 and 20 percent, and the second between 20 and 30 percent. In the laboratory these two stem sections were debarked and both wood and bark air dried and stored.

In the laboratory the number of annual rings at stump height was recorded, and the characterization disks air dried and stored. Each moisture disk was weighed green, its volume measured by water immersion, and its bark thickness (as measured by diameter tape before and after debarking) recorded. The debarked disk was weighed and its volume recorded. Heartwood was indicated by application of ferric chloride solution (10 g FeCl in 90 g water) and split away from the sapwood, heartwood diameter was measured, and heartwood weight and volume recorded. The oven-dry weights of bark, sapwood, and heartwood of each disk were then recorded.

Statistical Analyses

Analyses of variance were made in three groupings (table 1-2): *latifolia* throughout its principal latitudinal range of 40 through 60 degrees; *murrayana* through its primary latitudinal range of 37.5 through 45 degrees; and *latifolia* compared to *murrayana* at the three common latitudes of 40, 42.5, and 45 degrees.

For each of the two varieties, standard deviations for tree characteristics are noted in the text (in parentheses following average values); such notations are made only by diameter class, with all other factors pooled.

Correlations of interest observed in *latifolia* between tree characteristics are also noted in each discussion in the results section of the report.

1-7 TREE CHARACTERISTICS, DIMENSIONS, AND CUBIC VOLUMES

Previous sections provide a general introduction to this entire work. Subsequent sections in this chapter focus on tree characteristics, dimensions, and cubic volumes.

1-8 INTRODUCTION

Industrial managers concerned with the utilization of lodgepole pine need an understanding of general tree characteristics, dimensions, and cubic volumes. In partial satisfaction of such needs, this first chapter provides data on: taproot length, width of live crown, tree age, tree height to apical tip, tree height to 25-mm top diameter outside bark, length of live crown, length of stem below crown, stem crook, number of live branches, average diameter of live branches, average live branch angle, number of dead branches, crown ratio, average growth-ring width, total number of cones per tree, degree of cone serotiny, thickness of bark on stem and branches and roots, and volume and volume percentages of tree components—including both wood and bark of complete tree, live and dead branches, stem, stumps, and roots.

Table 1-2—Analyses of variance format

Source	Degrees of freedom	Source	Degrees of freedom	Source	Degrees of freedom
<i>Latifolia</i>		<i>Murrayana</i>		<i>Latifolia</i> compared to <i>Murrayana</i>	
Latitude (L)	8	Latitude	3	Variety (V)	1
Elevation (E)	2	Diameter	2	Latitude	2
Diameter (D)	2	L × D	6	Diameter	2
L × E	16	Error	24	V × L	2
L × D	16			V × D	2
E × D	4	Total	35	L × D	4
L × E × D	32			V × L × D	4
Error	162			Error	36
Total	242			Total	53

1-9 OBJECTIVE AND SCOPE

As previously noted, this characterization effort is confined to two varieties of lodgepole pine: *Pinus contorta* var. *latifolia* Engelm., and *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm., with emphasis on the former. The primary objective during tree collection was to obtain three replications of disease- and insect-free specimens of var. *latifolia* measuring 76, 152, and 228 mm in diameter at breast height (d.b.h.) at low, medium, and high elevations from nine equally spaced north latitudinal zones (40 to 60 degrees) across 10 degrees of longitude in such a way as to encompass the major range of this variety (fig. 1-1).

A secondary objective was to sample three replications of these same three diameter classes of var. *murrayana* at midelevation at four north latitudes (37.5, 40, 42.5, and 45 degrees) in California and Oregon at a single longitude per latitude (fig. 1-1).

The trees of both varieties were sampled in such a way that between-variety comparisons could be made for midelevation trees at latitudes 40, 42.5, and 45 degrees. The sampling plan does not permit computation of species-average values. The collection totaled 243 *latifolia* and 36 *murrayana* trees.

In this chapter variations in tree characteristics, dimensions, and cubic volumes are discussed. No attempt is made to construct equations for prediction of these properties. Instead, graphs are presented of data aggregated in various significant ways that permit readers to obtain information directly from the observed study data.

Explanations of statistical analyses procedures and a table of analyses of variance formats, with degrees of freedom indicated, are shown in table 1-2. In the results portion of this chapter standard deviations are noted in the text in parentheses following average values.

1-10 LITERATURE REVIEW

As previously noted, the literature lacks an overview of tree characteristics, dimensions, and cubic volumes related to latitude, elevational zone, diameter class, and longitudinal zone spanning the major range of lodgepole pine in North America. Because of this lack of characterization overview, literature related to this first chapter—which deals with a very large number of diverse characteristics—is not abstracted. Instead, table 1-1 lists peripherally pertinent references.

1-11 PROCEDURE

Procedural details of the study are given in section 1-6, and will not be repeated here except to note that the elevational zones of low, medium, and high are relative.

Medium refers to an elevation that is medium for the variety at the latitude at which sampled; similarly, low and high refer to lower and upper elevational zones in which the variety occurs at the latitude sampled. *Latifolia* elevational zones were highest in the south (2,481, 2,711, and 3,144 m at 40 degrees) and progressively lower with each more northerly latitude (604, 739, and 879 m at 60 degrees). *Murrayana* was sampled at elevations in the range from 1,148 to 2,402 m.

Trees were uprooted (with central taproot intact and with lateral roots severed at a radius of 305 mm from tree pith) from level benches in natural unthinned stands within National or Provincial Forests. The sampling scheme resulted in selection of 76-, 152-, and 228-mm trees averaging 71, 91, and 107 years of age, respectively, for *latifolia*, and 67, 84, and 91 years for *murrayana*. Most of the small-diameter trees were suppressed, while the larger trees were the fast growers.

Readers of these results should keep in mind that the three diameter classes (76 mm with standard deviation of 1.96 mm; 152 mm with standard deviation of 2.49 mm; and 228 mm with standard deviation of 2.97 mm) were selected in such a manner that trees were usually sampled in groups of three (one from each diameter class) from each bench sampled, and that frequently the stands were of fire origin and therefore somewhat uniform in age. Thus, the 76-mm trees averaged 71 years of age at stump height, the 152-mm trees 91 years, and the 228-mm trees 107 years of age. This age distribution suggests that the 76-mm class represents somewhat suppressed trees, while the 228-mm trees were relatively fast growers in the stands selected.

Additionally, readers should remember that the sample extended from almost the extreme southern end of the range to almost the extreme northern end of the range—midpoint of the samples was 50 degrees (fig. 1-1). Elevational zones were much higher in the south (near 3,000 m) than in the north where they were less than 1,000 m (fig. 1-3).

Longitudinal effects on *latifolia* were confounded with latitudinal effects (the northern latitudinal zones were further west than the southern latitudinal zones). When each latitudinal zone was divided into 10 longitudinal zones, each a degree of longitude wide, and expressed by a number from 1 to 10 going from east to west, no significant longitudinal effects were found for any characteristic.

1-12 RESULTS—LATIFOLIA

In the paragraphs that follow, only those main effects and interactions shown statistically significant (5 percent level) by analyses of variance are discussed, tabulated, and graphed.

Tree Age

As noted above, the three diameter classes averaged (with standard deviations in parentheses following) 71 (27), 91 (31), and 107 (39) years of age measured at 152 mm stump height. Trees averaged oldest at high elevation (103 years) and youngest at low elevation (75 years); at medium elevation average age was intermediate at 91 years, but variations in this trend were evident by latitude (fig. 1-5). Tree age throughout all latitudes averaged 90 years but was greatest at the two latitudinal extremes—94 years at 40 degrees and 116 years at 60 degrees; it was minimum (78 years) at 45 degrees.

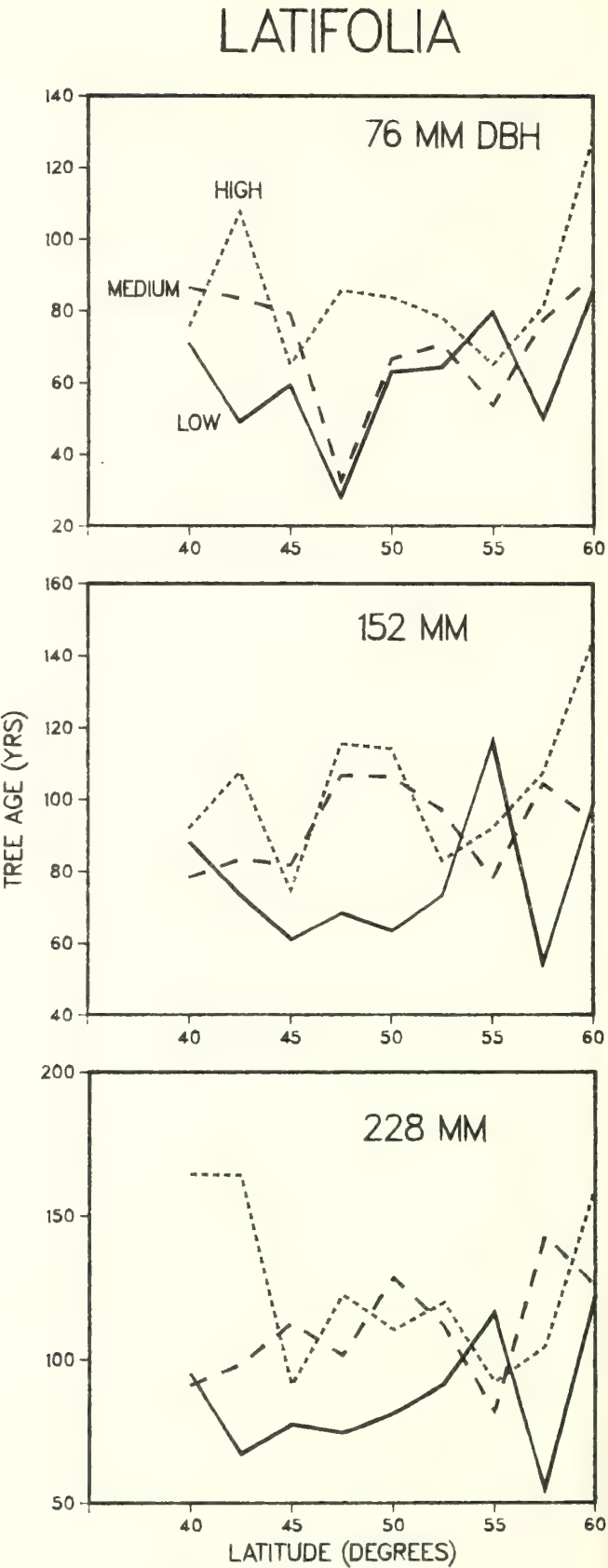


Figure 1-5—Tree age at 152-mm-high stump level related to elevational zone and latitude for *latifolia* trees of three diameters.

Tree Height to Apical Tip

The three diameter classes averaged 9.3 (2.0), 15.6 (2.5), and 19.1 (3.0) m in height from 152-mm-high stump to apical tip; this height varied significantly with both latitude and elevation; trees were tallest at latitudes 50, 52.5, and 55 degrees (fig. 1-6). Except in the middiameter class, trees were tallest at low elevation and shortest at high elevation, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
	-----	m-----	
76	9.7	9.4	8.7
152	15.7	15.9	15.1
228	20.0	19.1	18.2
Average	15.1	14.8	14.0

Tree height to apical tip was positively correlated with taproot length (0.60), number of live branches (0.63), average branch angle (0.60), and volume of wood plus bark in the stump-root system (0.81); it was negatively correlated with the stembark percentage of gross stem volume (-0.81), and treebark percentage of gross tree volume (-0.83).

Tree Height to 25-mm Top Diameter (Outside Bark)

Tree height from 152-mm-high stump to a diameter outside bark of 25 mm is of interest to roundwood products producers. This height averaged 8.0 (1.9), 14.7 (2.5), and 18.3 (2.9) m for the three diameter classes, but varied significantly with both latitude and elevation class. Trees were generally tallest to the 25-mm dimension in latitude zones 50, 52.5, and 55 degrees (fig. 1-7). Except for the 152-mm trees, trees were tallest in low-elevation and shortest in high-elevation zones, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
	-----	m-----	
76	8.3	8.2	7.6
152	14.7	15.1	14.3
228	19.1	18.4	17.5

Tree height to 25-mm top diameter was positively correlated with taproot length (0.60), number of live branches (0.63), live branch angle (0.61), and volume of wood plus bark in the stump-root system (0.80); it was negatively correlated with stembark percentage of gross stem volume (-0.81), and with bark percentage of gross tree volume (-0.83).

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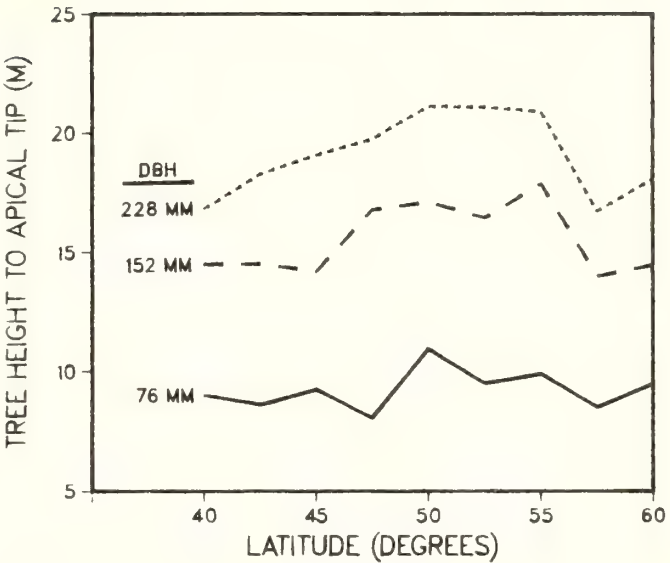


Figure 1-6—Tree height from 152-mm-high stump top to apical tip related to latitude for latifolia trees of three diameters.

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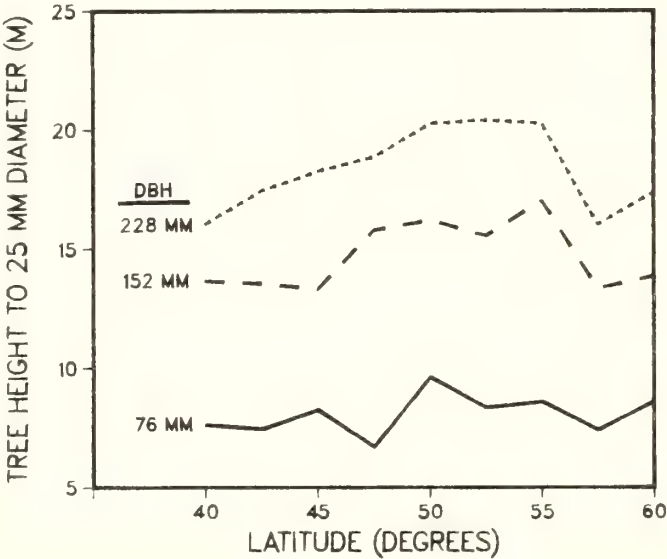


Figure 1-7—Tree height from stump top to 25-mm top diameter (measured outside bark) for latifolia trees of three diameters.

Taproot Length

Taproot length, measured from stump top to the end of the portion of taproot the field crews were successful in extracting (fig. 1-4), was positively correlated with d.b.h., and averaged 55.4 (16.7), 77.8 (20.5), and 94.2 (21.6) cm for the three diameter classes. Taproot lengths were generally longer in southern latitudes, with maximum lengths occurring near 47.5 degrees (fig. 1-8). Except for the 76-mm trees, taproots were longest in low-elevation and shortest in high-elevation zones, as follows:

D.b.h.	Elevation zone		
	Low	Medium	High
<i>mm</i>		<i>m</i>	
76	53.3	60.2	52.6
152	83.7	76.4	73.3
228	103.7	98.3	80.6

Taproot length was positively correlated with both height to apical tip and to 25-mm top diameter (both 0.60), growth-ring width at stump height (0.53), and wood volume of complete tree (0.62).

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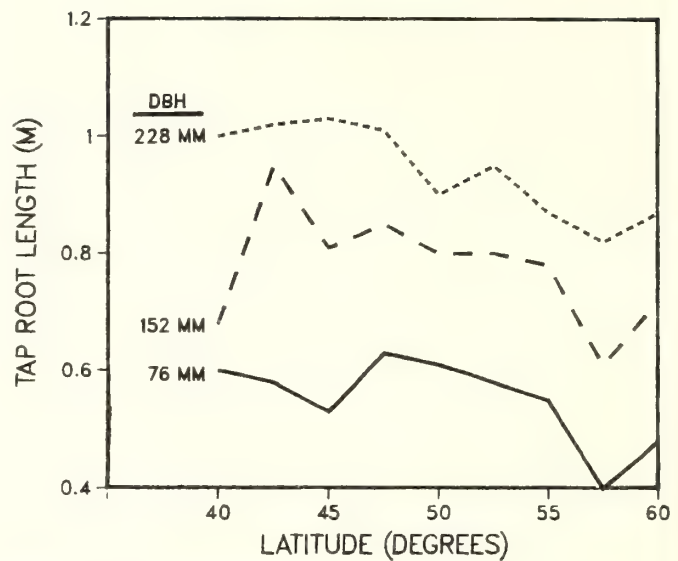


Figure 1-8—Taproot length from stump top to the bottom end of that portion of the taproot field crews were successful in extracting related to latitude for *latifolia* trees of three diameters.

Width of Live Crown

Crown width was unrelated to latitude, but was positively correlated with d.b.h.—averaging 1.16 (0.32), 1.81 (0.36), and 2.85 (0.74) m for the three diameter classes, and negatively correlated with elevation zones, as follows:

D.b.h.	Elevation zone		
	Low	Medium	High
<i>mm</i>	<i>m</i>		
76	1.22	1.15	1.12
152	1.93	1.83	1.68
228	2.95	3.00	2.60
Average	2.03	1.99	1.80

Crown width was positively correlated with tree height (0.58), taproot length (0.54), average diameter of live branches (0.73), average ring width at stump height (0.52), stembark thickness at 50 percent of tree height (0.71), total live branch volume (0.87), gross volume of the stump-root system (0.81), stemwood volume (0.77), and live branchwood percentage of wood volume in the complete tree (0.64). It was negatively correlated with live branch-bark percentage of gross live branch volume (-0.69).

Length of Live Crown

Crown length was positively correlated with d.b.h., averaging 4.21 (1.57), 6.73 (2.48), and 8.24 (2.59) m for the three diameter classes. Elevational effects varied with latitude, with no clear trend evident. For the two smaller diameter classes, crowns were shorter in northern latitudes than in southern (fig. 1-9).

Length of live crown was also positively correlated with taproot length (0.53), number of live branches (0.63), average ring width at stump height (0.55), gross volume of live branches (0.56), stemwood volume (0.53), and bark volume of the complete tree (0.58). It was poorly correlated with branch diameter (0.38) or branch angle (-0.27).

LATIFOLIA

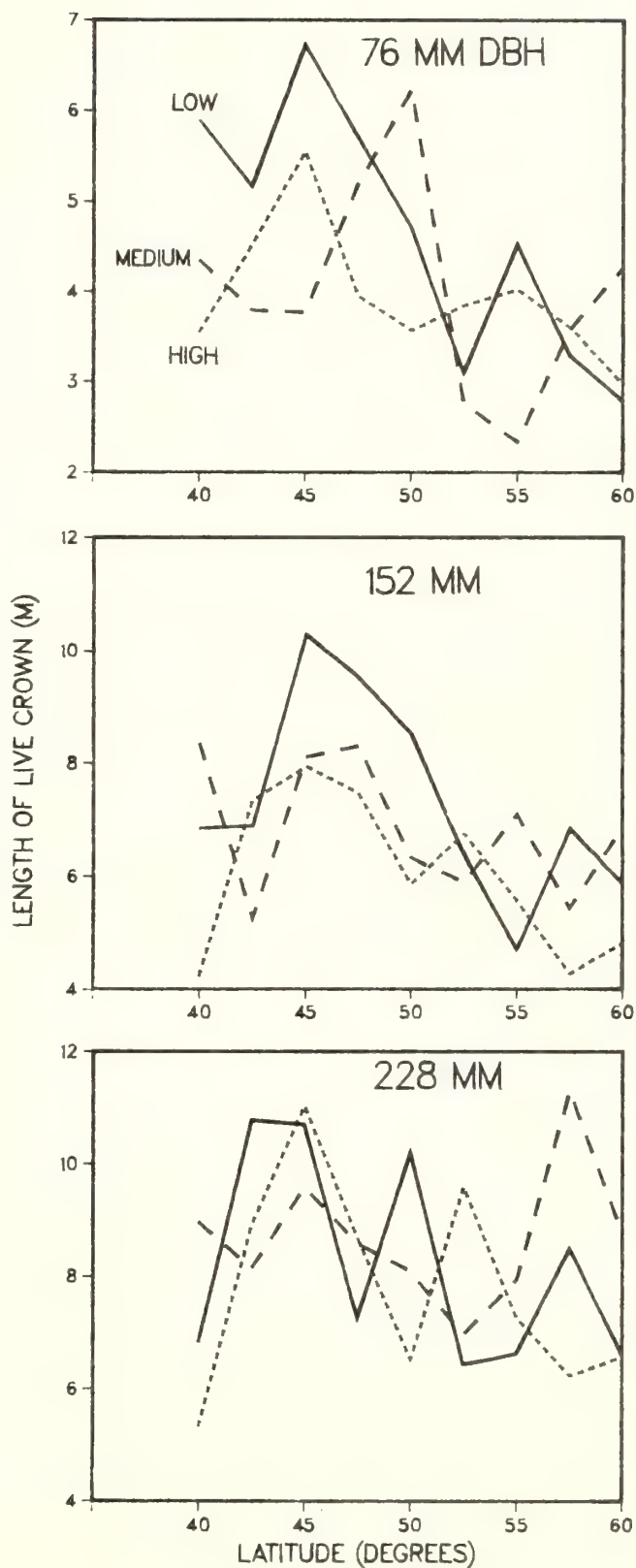


Figure 1-9—Length of live crown related to elevational zone and latitude for *latifolia* trees of three diameters.

Length of Stem Below Crown

Stem length below crown was positively correlated with tree diameter, averaging 5.03 (2.53), 8.82 (3.43), and 10.85 (3.83) m for the three diameter classes. Latitudes 50, 52.5, and 55 degrees had trees with the longest stem lengths below crowns (fig. 1-10).

Length of stem below crown was negatively correlated with stembark percent of gross stem volume (-0.67) and crown ratio (-0.69). It was positively correlated with wood-plus-bark volume of the stump-root system (0.56) and with stemwood volume (0.68).

Stem Crook

Stem crook between 10 and 70 percent of tree height averaged 43 mm, with standard deviation of 24.5 mm, and was unrelated to tree diameter or elevational zone. Trees within latitude zones 47.5 through 55 degrees averaged only 38 mm of stem crook, while the other five latitudinal zones averaged 48 mm stem crook (fig. 1-11). We measured the percentage of tree height where maximum stem crook occurred, but found its location was unrelated to any of the factors in the study; the average location was at 40 percent of tree height from stump top to apical tip.

Stem crook had a significant, but slight, positive correlation with tree age (0.21).

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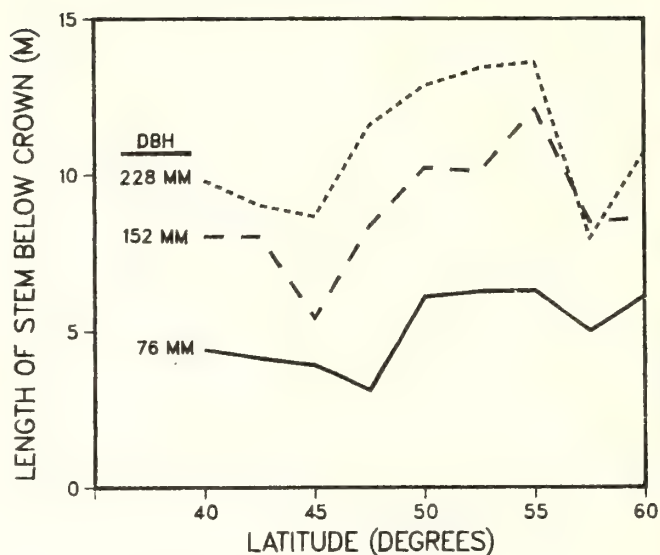


Figure 1-10—Length of stem below crown related to latitude for *latifolia* trees of three diameters.

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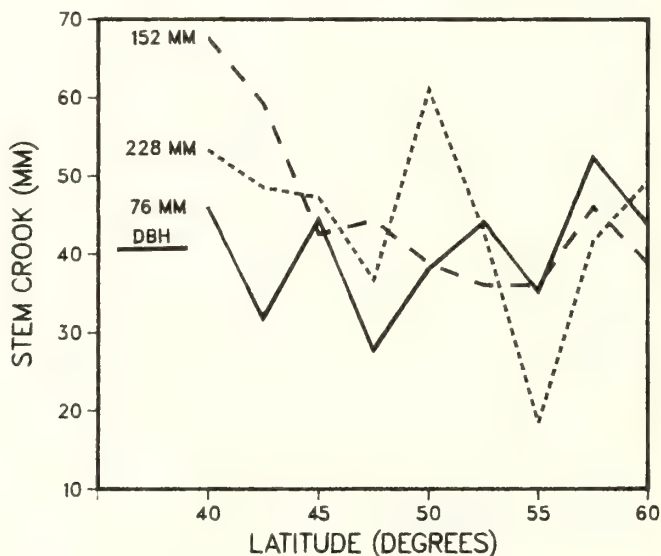


Figure 1-11—Maximum stem crook (sweep), measured perpendicular to a taut string placed against stem periphery at 10 percent of tree height and stretched to 70 percent of tree height related to latitude for *latifolia* trees of three diameters.

Number of Live Branches

The number of live branches per tree was positively correlated with d.b.h., averaging 64 (27), 108 (36), and 133 (36) for the three diameter classes. Trees at latitudes 47.5 and 60 degrees had fewer live branches than those at the other seven latitudes; those at 50 degrees had most live branches (fig. 1-12).

The number of live branches was also positively correlated with tree height (0.63), crown length (0.63), and wood-plus-bark volume of the stump-root system (0.62), and with wood and bark volume of the complete tree (0.65).

Average Diameter of Live Branches
(50 mm From Stem)

Mean branch diameter outside bark was unrelated to elevational zone but was positively correlated with d.b.h., averaging 9 (2.0), 13 (2.9), and 19 (4.0) mm for the three tree diameter classes. Trees at 50 degrees latitude averaged smallest branches (12 mm), while those at 60 degrees had the largest, averaging 16 mm (fig. 1-13).

Average diameter of live branches was negatively correlated with live branchbark percent of gross live branch volume (-0.82) and with branch angle (-0.29). It was positively correlated with tree height (0.59), crown width (0.72), number of cones on the top 25 branches (0.52), branchbark thickness (0.59), stembark thickness at 50 percent of tree height (0.71), total volume of live branchwood (0.78), volume of wood plus bark in the stump-root system (0.81), and volume of wood plus bark in the stem (0.77).

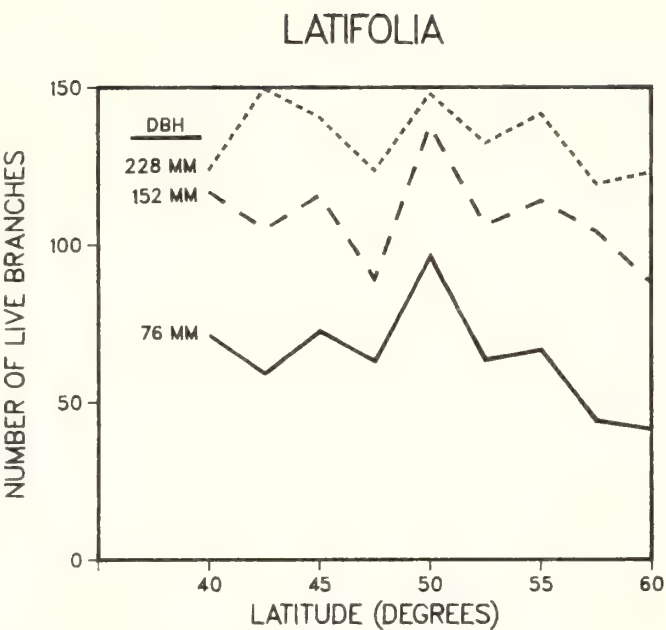


Figure 1-12—Number of live branches on *latifolia* trees related to latitude and d.b.h.

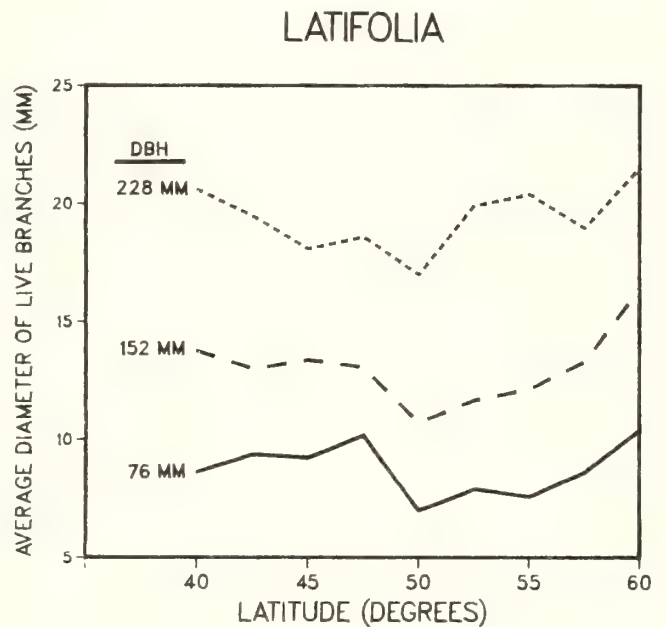


Figure 1-13—Average diameter of live branches, measured outside bark and 50 mm from stem surface, related to latitude for *latifolia* trees of three diameters.

Average Live Branch Angle

The average angle between live branches and stem (upward-pointing branches had angles less than 90 degrees; those with drooping branches more than 90 degrees) was larger in small trees than large, and averaged 85 (12.5), 79 (10.0), and 77 (10.5) degrees for the three diameter classes. In latitude zones 50 and 52.5 degrees, trees in the high-elevation zone had larger branch angles than those in the low-elevation zone, while at 45 degrees the reverse was true (fig. 1-14).

Average live branch angle was negatively correlated with branch diameter (-0.29) and average ring width at stump height (-0.41).

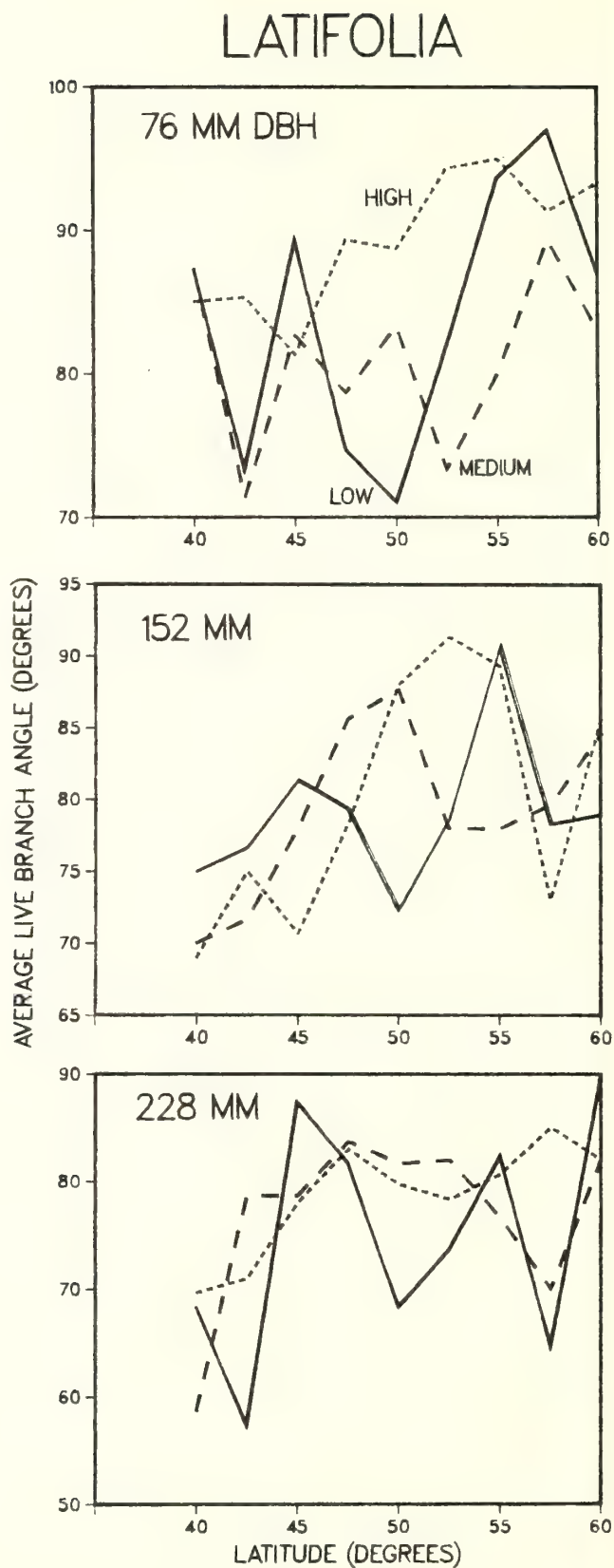


Figure 1-14—Average live branch angle, measured between stem surface above branch and branch upper surface at point of entry to stem, related to elevational zone and latitude for *latifolia* trees of three diameters.

Number of Dead Branches

The number of dead branches per tree was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 57 (36), 100 (43), and 119 (53) for the three diameter classes. Fewest were observed in latitudes 42.5 through 47.5 degrees (average 72), and most in latitudes 50 through 57.5 degrees, where trees averaged 106 dead branches per tree (fig. 1-15).

The number of dead branches was also positively correlated with tree height (0.53), stem length below crown (0.57), and with wood-plus-bark volume of the stump-root system (0.49). It was negatively correlated with treebark percentage of gross tree volume (-0.55).

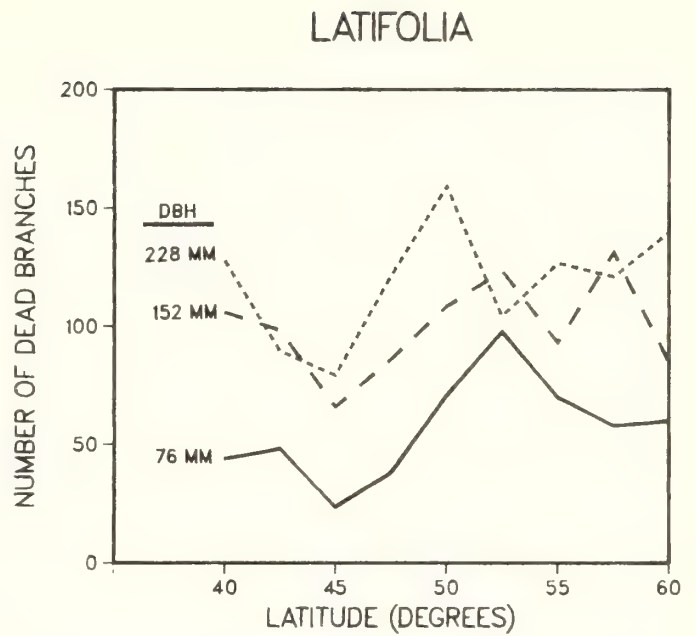


Figure 1-15—Number of dead branches on *latifolia* trees related to latitude and d.b.h.

Stem Diameter (Bark-Free) at Base of Live Crown

Stem diameter at the base of the live crown was proportional to d.b.h., averaging 52 (11.4), 100 (18.5), and 148 (23.1) mm for the three diameter classes. This below-crown diameter tended to be larger in southern latitudes than northern—particularly in the two smaller d.b.h. classes (fig. 1-16)—probably because crown ratios in the south were larger than in the north (fig. 1-17).

Crown Ratio

Crown ratio, the ratio of crown length to tree height from stump top to apical tip, is of primary interest to tree physiologists while stem ratio (1.0 - crown ratio) is of interest to those who convert trees to products. Because stem ratio is easily calculated from crown ratio, only data on the latter are reported here.

Crown ratio was unrelated to tree diameter, averaging 0.456 for all *latifolia* trees, with standard deviation of 0.168. It was inversely related to elevational zone, with averages of 0.470, 0.453, and 0.446 for low, medium, and high zones, but the effect varied with latitude (fig. 1-17). Averages for latitudinal zones were lowest at 52.5 and 55 degrees, and highest at 40 through 47.5 degrees, as follows:

Latitudinal zone	Crown ratio
Degrees	
40	0.474
42.5	.499
45	.576
47.5	.527
50	.431
52.5	.368
55	.376
57.5	.446
60	.410

Crown ratio was positively correlated with crown length (0.49) and negatively correlated with stem length below crown (-0.69).

Average Growth-Ring Width at 152-mm Stump Height

As expected, because the small trees were suppressed and the large trees were the fast growers in most stands selected, growth-ring width was positively related to d.b.h., averaging 0.67 (0.35), 1.01 (0.35), and 1.33 (0.46) mm for the three diameter classes. Ring width varied inversely with elevational zone and averaged 1.19, 0.96, and 0.86 mm for low, medium, and high zones—but the relationship differed with latitude (fig. 1-18). Ring width averaged widest at 47.5 degrees (1.23 mm) and least at 60 degrees (0.72 mm).

Average growth-ring width at stump height was positively correlated with taproot length (0.53), crown length (0.55), dead branch volume (0.53), total live branch volume (0.52), volume of wood plus bark in the stump-root system (0.57), and volume of wood plus bark in the stem (0.53).

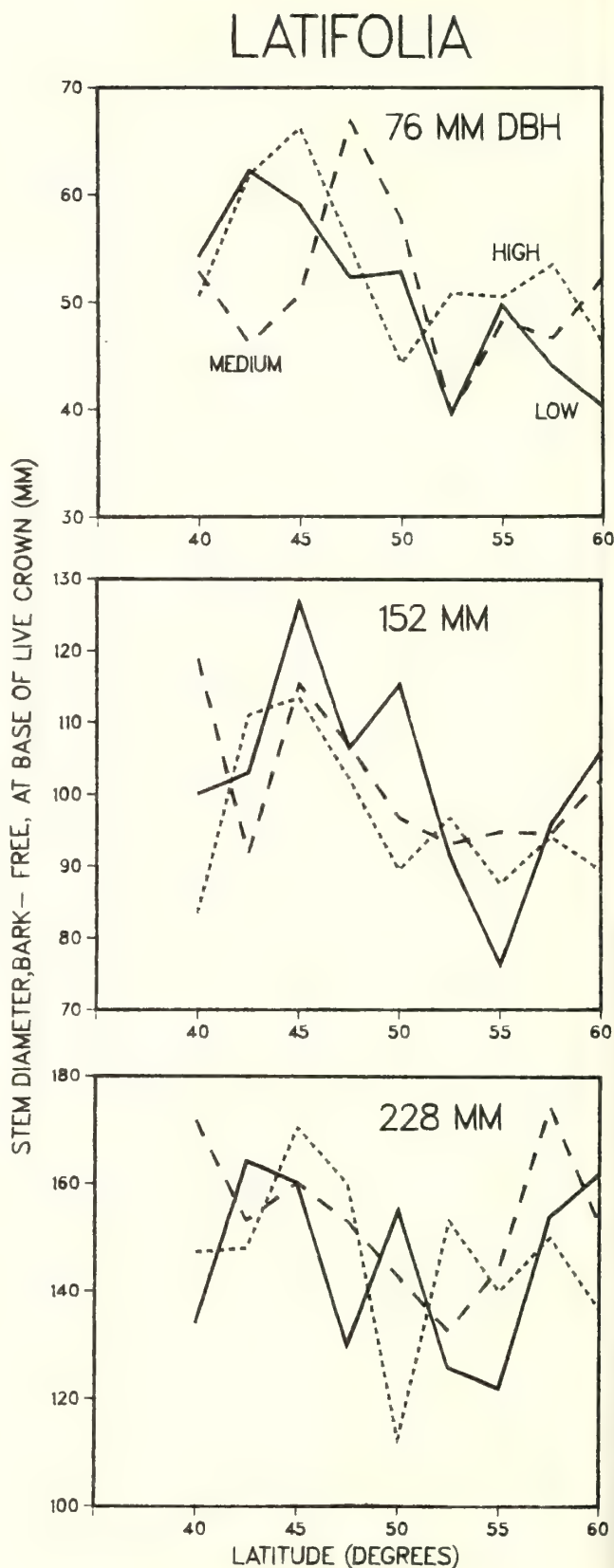
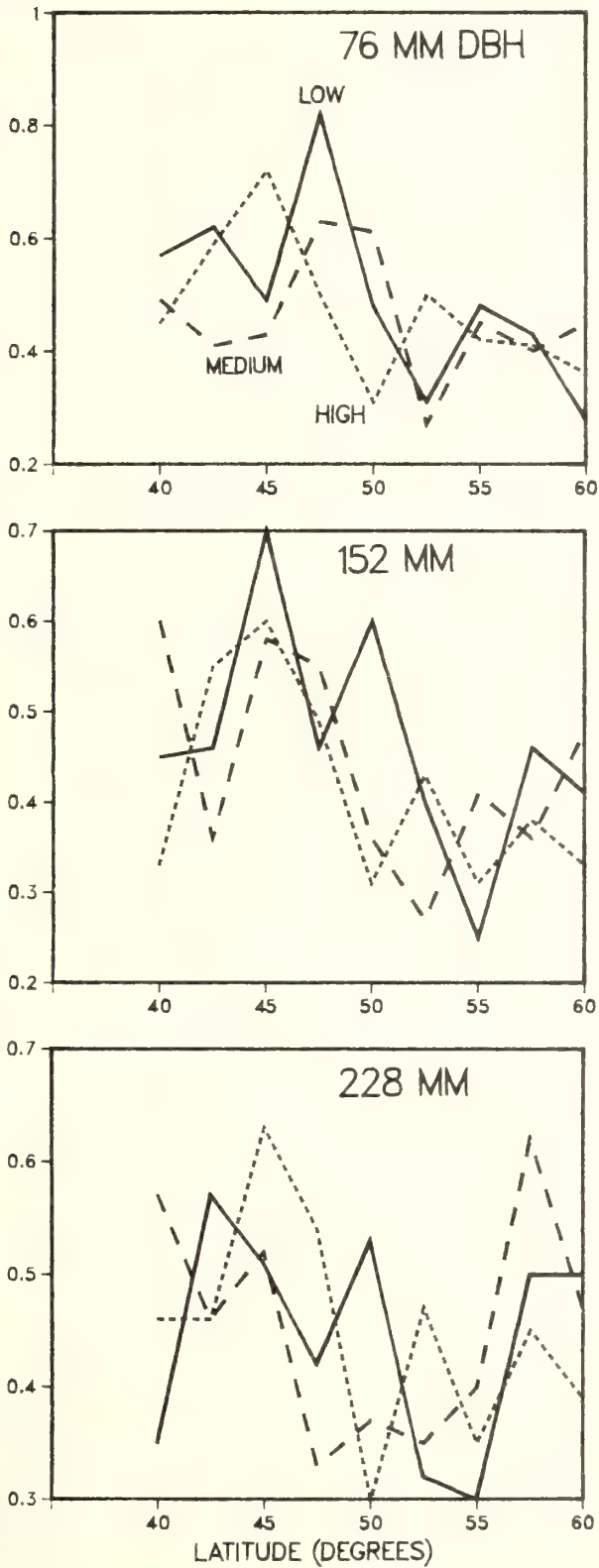


Figure 1-16—Stem diameter, measured inside bark at base of live crown, related to elevational zone and latitude for *latifolia* trees of three d.b.h. classes.

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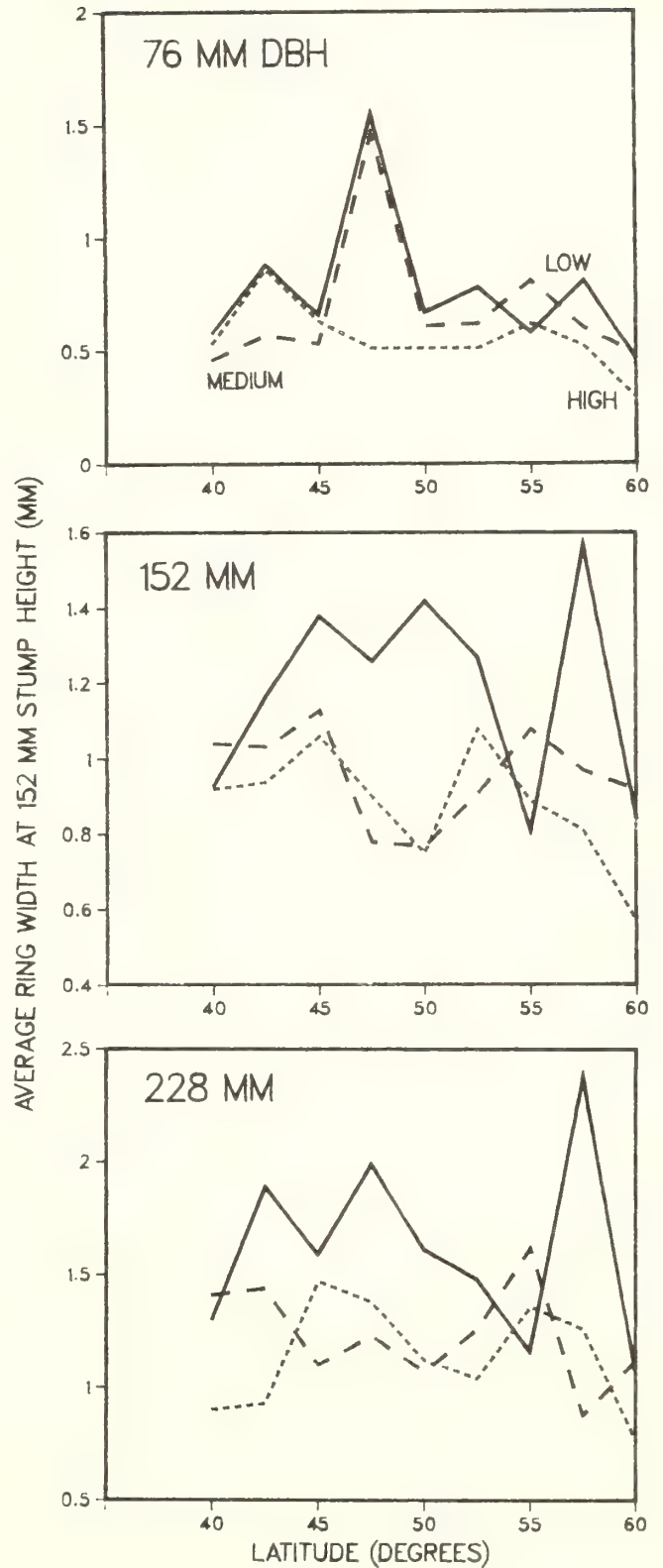


Figure 1-17—Crown ratio (crown length/tree height) related to elevational zone and latitude for *latifolia* trees of three diameters.

Figure 1-18—Average width of growth rings, measured at stump height, related to elevational zone and latitude for *latifolia* of three diameters.

Number of Cones on the Tip 305 mm of the Top 25 Branches

Only 191 of the 243 trees had cones on the tip 305 mm of the top 25 branches. Aggregate cone numbers on these 25 branches were unrelated to latitudinal or elevational zone, but were positively correlated with d.b.h., averaging 6 (19), 35 (32), and 78 (62) cones for the three diameter classes.

Number of cones on the tip 305 mm of the top 25 branches was positively correlated with the wood-plus-bark volume of the stump-root system (0.55), average branch diameter (0.52), total live branch volume (0.46), and the wood-plus-bark volume of the stem (0.58).

Total Number of Cones per Tree (Calculated)

The calculated number of cones per tree was unrelated to latitudinal or elevational zones, but was positively correlated with d.b.h., averaging 32 (86), 160 (154), and 555 (587) cones per tree for the three diameter classes. These averages are low because they reflect the fact that not all of the 243 trees had cones on the tip 305 mm of the top 25 branches—the basis for computation of tree totals.

Cone Serotiny

The number of trees with cones on the top 25 branches was positively correlated with d.b.h., numbering 37, 74, and 80 for the three diameter classes—for a total of 191 out of the total 243 *latifolia* trees. The number of cone-bearing trees was unrelated to elevational zone, and averaged 21 trees out of 27 per latitude, varying from a minimum of 16 at 47.5 degrees to a maximum of 26 at 60 degrees.

Of these 191 trees with cones, 62.3 percent had predominantly serotinous (closed) cones and 25.7 percent had predominantly open cones; the remaining 12 percent was intermediate. A greater percentage of cone-bearing trees in lower elevational zones had serotinous cones, and a lesser percentage had open cones, than trees in high-elevation zones, as follows:

Elevational zone	Serotinous	Open
	----- Percent -----	
Low	67.1	20.2
Medium	65.8	21.3
High	57.3	34.9

A greater percentage of cone-bearing trees of small d.b.h. had serotinous cones than trees of large d.b.h.; percentage of open-coned trees was unrelated to d.b.h., however, as follows:

D.b.h. class	Serotinous	Open
mm	----- Percent -----	
76	65.3	25.4
152	60.7	27.1
228	59.9	23.8

At all latitudes the proportion of cone-bearing trees with intermediate cones (neither predominantly open nor predominantly closed) was more or less constant in the range from 10 to 20 percent. The percentage of trees with serotinous cones exceeded the percentage with open cones at all latitudes except 42.5 and 45 degrees, but the proportion of trees with predominantly serotinous cones increased with increasing latitude; at latitudes of 52.5 through 60 degrees, virtually all cone-bearing trees had serotinous cones (fig. 1-19).

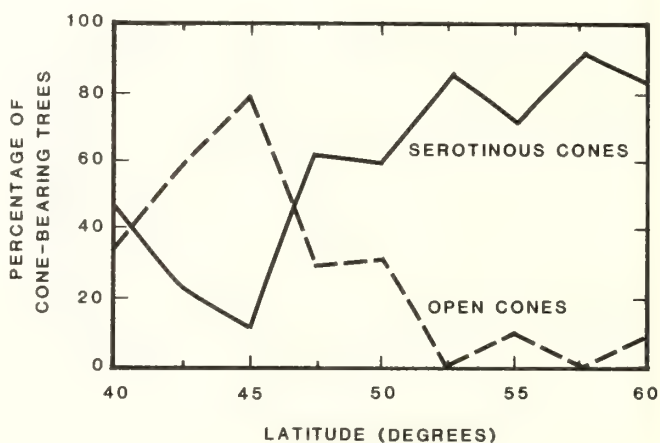


Figure 1-19—Latitudinal zone related to percentage of cone-bearing *latifolia* trees having predominantly serotinous (closed) cones and predominantly open cones. Remaining trees (10 to 20 percent) carried a mixture of serotinous and open cones.

Branchbark Thickness (Measured With a Scale)

Except for latitudes 45 and 47.5 degrees, branchbark thickness was positively correlated with d.b.h., averaging 1.1 (0.19), 1.2 (0.28), and 1.5 (0.33) mm for the three diameter classes (fig. 1-20). Bark averaged thinnest (1.1 mm) at 40 and 50 degrees latitude, and thickest (1.5 mm) at latitude 57.5 degrees.

Branchbark thickness was also positively correlated with crown width (0.43), live branch diameter (0.59), bark thickness on lateral roots (0.43), stembark thickness at 50 percent of tree height (0.57), volume of live branchbark (0.56), and wood-plus-bark volume of the stump-root system (0.49).

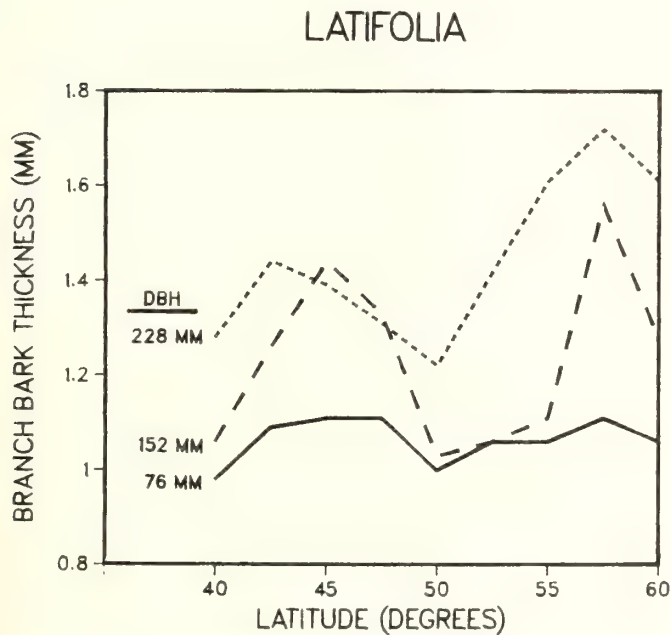


Figure 1-20—Branchbark thickness related to latitude for *latifolia* trees of three diameters.

Central Rootbark Thickness (Measured With a Scale)

Bark thickness of the central taproot was positively correlated with d.b.h., averaging 3.1 (1.00), 4.5 (1.38), and 5.8 (1.76) mm for the three diameter classes. Bark averaged thinnest at low elevation (4.4 mm) and at 55 degrees latitude (3.8 mm); it was thickest at high elevation (4.5 mm) and at 57.5 degrees latitude (5.2 mm), but the interaction between elevation and latitude was complex (fig. 1-21).

Central rootbark thickness was negatively correlated with live branchbark percentage of gross live branch volume (-0.48). It was positively correlated with crown width (0.57), live branch diameter (0.54), lateral rootbark thickness (0.71), stumpbark thickness (0.69), stembark thickness at 50 percent of tree height (0.60), total live branch volume (0.59), wood volume in the stump-root system (0.59), bark volume in the stump-root system (0.66), and bark volume in the complete tree (0.63).

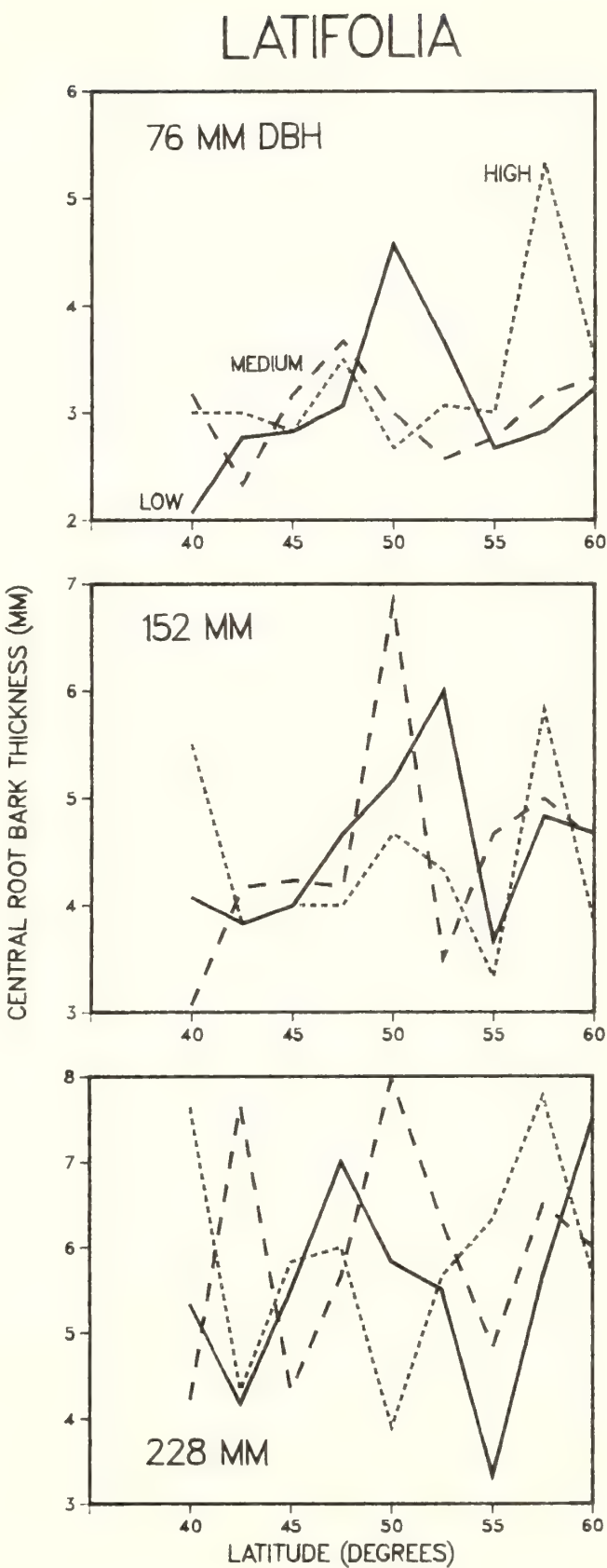


Figure 1-21—Bark thickness of the central taproot related to elevational zone and latitude for *latifolia* trees of three diameters.

Lateral Rootbark Thickness (Measured With a Scale)

Bark thickness of the lateral roots within a few inches of the root collar was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 2.2 (0.60), 3.3 (1.01), and 4.6 (1.32) mm for the three diameter classes. Bark was thinnest (average 3.2 mm) in the five southern latitudinal zones and thickest (3.6 mm) in the four northernmost zones (fig. 1-22).

Lateral rootbark thickness was negatively correlated with live branchbark percentage of gross live branch volume (-0.50). It was positively correlated with tree height (0.47), crown width (0.59), live branch diameter (0.59), branchbark thickness (0.43), bark thickness of central root (0.71), stumpbark thickness (0.72), stembark thickness at 50 percent of tree height (0.66), total live branch volume (0.65), wood-plus-bark volume of stump-root system (0.65), and bark volume of the stump-root system (0.70).

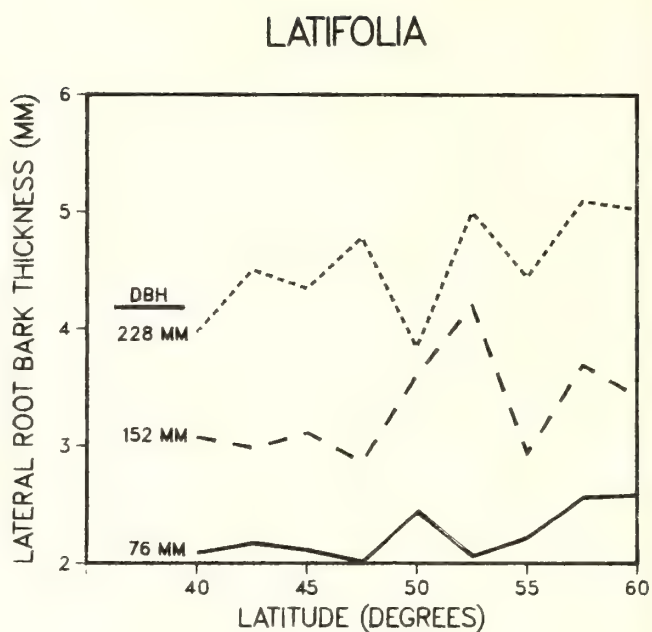


Figure 1-22—Lateral rootbark thickness related to latitude for *latifolia* trees of three diameters.

Stumpbark Thickness (Measured With a Scale)

Bark thickness of the stump between groundline and 152-mm stump height was positively correlated with d.b.h., averaging 4.2 (1.20), 6.8 (2.83), and 8.6 (2.79) mm for the three diameter classes. Bark averaged thickest in low-elevation zones (7.0 mm) and in midlatitude zones (7.6 mm); it averaged thinnest in high-elevation zones (6.2 mm) and in the three southern or three northern latitudinal zones (6.0 mm). Interactions between elevational and latitudinal zones were complex, however (fig. 1-23).

Stumpbark thickness was also positively correlated with crown width (0.55), thickness of central rootbark (0.70), thickness of lateral rootbark (0.72), thickness of stembark at 50 percent of tree height (0.57), total live branch volume (0.55), and wood-plus-bark volume of the stump-root system (0.57). It was only weakly correlated with branchbark thickness (0.27).

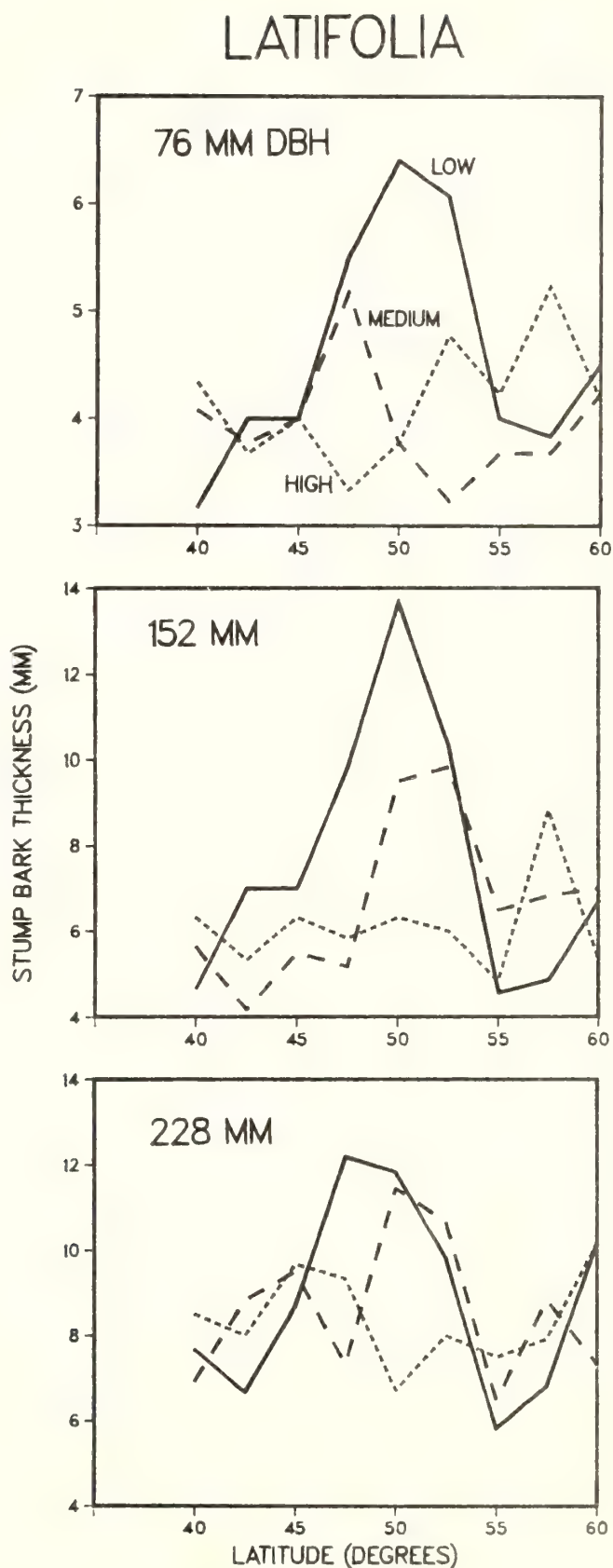


Figure 1-23—Stumpbark thickness, averaged from groundline to 152-mm-high stump top, related to elevational zone and latitude for *latifolia* trees of three diameters.

Stembark Thickness (Measured With a Diameter Tape)

Stembark thickness was measured from stump level (0 percent tree height) to 90 percent of height to apical tip, at 10-percent intervals. Tree d.b.h. and height in stem were the dominant variables related to stembark thickness; bark was thickest at stump level and diminished in ogee pattern with increased height in tree, and with tree d.b.h. (fig. 1-24). Pooling all elevation, latitude, and height-in-tree classes, stembark thickness averaged 2.4, 3.7, and 4.9 mm for the three diameter classes.

Only at stump height was stembark thickness inversely related to elevation class; i.e., with all other factors pooled, bark at stump height was 7.5 mm thick at low, 6.3 mm at medium, and 6.1 mm thick at high elevation. At all higher levels in the stem, stembark thickness was about equal at medium and high elevation, but was consistently 0.1 or 0.2 mm thinner at low elevation than in the other two elevation classes.

With stembark thickness averaged for all heights in the stem, latitudinal effects were minor (fig. 1-25).

Stembark thickness at 50 percent of tree height was positively correlated with height to 25 mm top diameter (0.58), crown width (0.70), crown length (0.47), number of live branches (0.53), live branch diameter (0.71), growth-ring width at stump height (0.43), number of cones on the top 25 branches (0.52), branchbark thickness (0.57), central rootbark thickness (0.60), lateral rootbark thickness (0.66), stumpbark thickness (0.57), total live branch volume (0.76), total stump-root system volume (0.78), and stembark volume (0.82).

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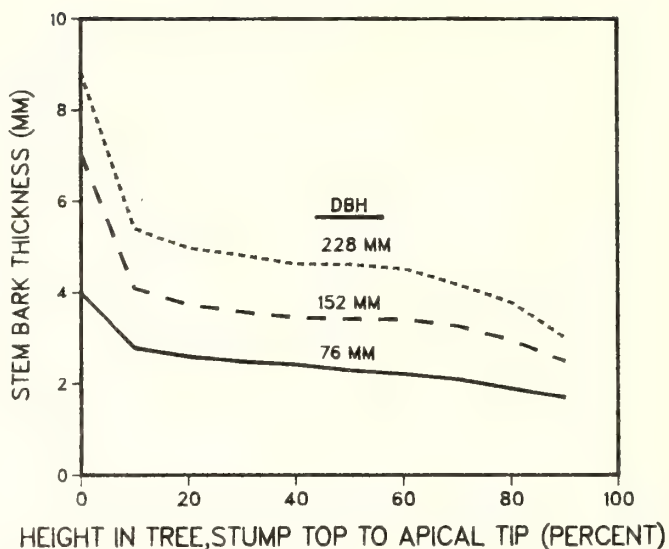


Figure 1-24—Stembark thickness related to height in *latifolia* trees of three diameters.

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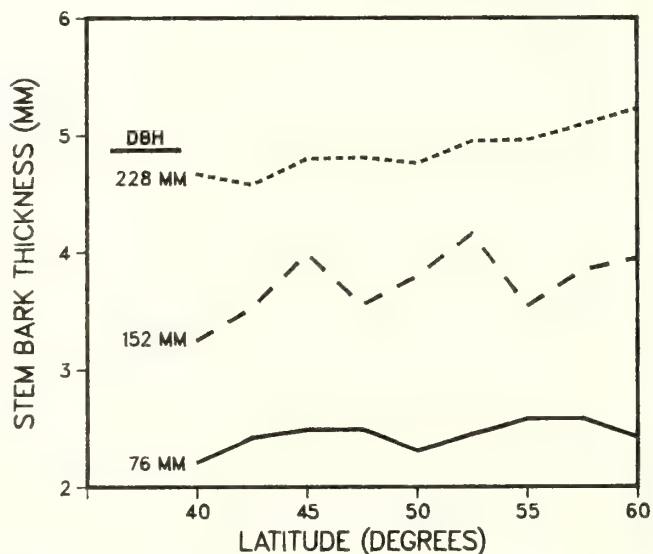


Figure 1-25—Stembark thickness, averaged from stump height to 90 percent of tree height, related to latitude for *latifolia* trees of three diameters.

Total Volume of Dead Branches (Thousand cm³)

Volume of dead branches was positively correlated with d.b.h., averaging 0.5 (0.40), 3.4 (2.87), and 10.2 (9.40) for the three diameter classes. High-elevation trees had less volume of dead branches than low-elevation trees, as follows:

D.b.h.	Elevation class		
	Low	Medium	High
mm	----- Thousand cm ³ -----		
76	0.7	0.5	0.4
152	4.5	3.1	2.7
228	13.9	9.9	6.7
Average	6.4	4.5	3.3

The effect of latitude varied with diameter and elevation class (fig. 1-26). At 57.5 degrees, all 152-mm trees had average dead-branch volume of 7.15; at the other eight latitudes, dead-branch volume for this diameter class (elevations pooled) averaged much less—in the range from 2.2 to 3.7.

Dead-branch volume was positively correlated with crown width (0.50), average ring width at stump height (0.53), total live branch volume (0.59), total root system volume (0.58), and total stem volume (0.54).

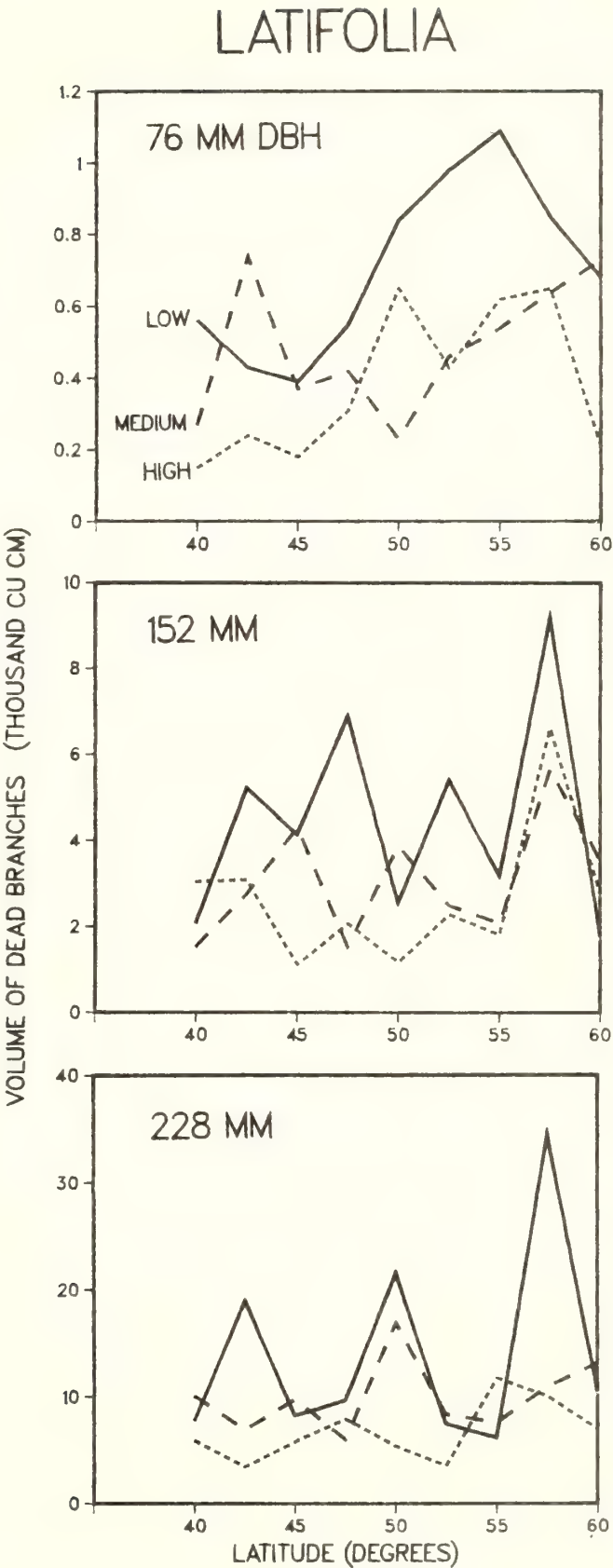


Figure 1-26—Volume of dead branches of *latifolia* trees of three diameters related to elevational zone and latitude.

Volume of Live Branches, Wood Plus Bark (Thousand cm³)

Total volume was positively correlated with d.b.h., averaging 1.5 (0.81), 10.2 (4.37), and 35.9 (15.15) for the three diameter classes. Volume varied inversely with elevation, averaging (with all latitudes and diameters pooled) 17.6, 16.3, and 13.6 for low-, medium-, and high-elevation classes; for the 76-mm diameter class, latitude interacted with elevation, however (fig. 1-27).

Total live branch volume was also negatively correlated with live branchbark percentage of gross live branch volume (-0.66). It was positively correlated with tree height (0.56), length of taproot (0.52), width of crown (0.87), length of crown (0.50), number of live branches (0.50), live branch diameter (0.77), average growth-ring width at stump height (0.52), branchbark thickness (0.55), lateral rootbark thickness (0.65), stembark thickness at 50 percent of tree height (0.76), dead branch volume (0.60), total stump-root system volume (0.84), and total stem volume (0.77).

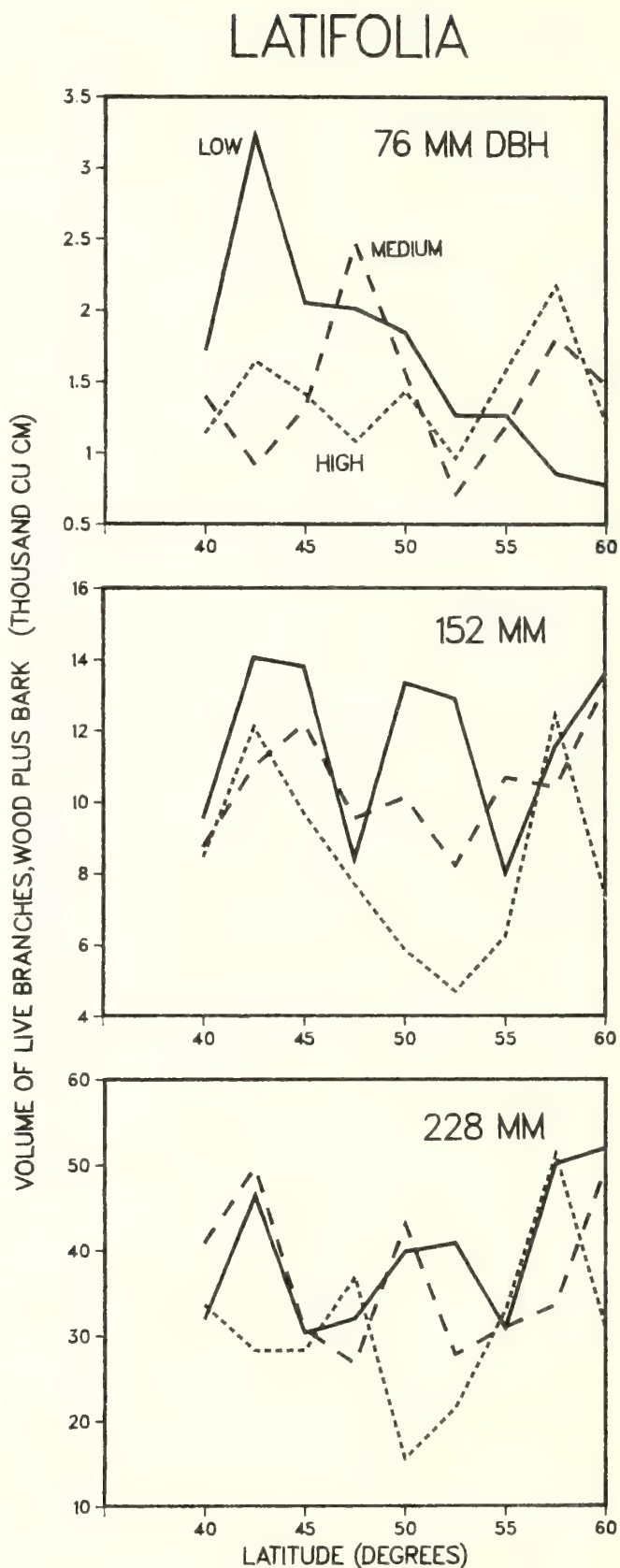


Figure 1-27—Live-branch volume, wood plus bark, of *latifolia* trees of three diameters related to elevational zone and latitude.

Volume of Live Branchwood (Thousand cm³)

Live branchwood volume was positively correlated with d.b.h., averaging 0.8 (0.45), 6.4 (2.81), and 25.5 (11.27) for the three diameter classes. Volume tended to vary inversely with elevation, particularly for the 152-mm trees; with all diameter and latitude values pooled, averages were 12.2, 11.3, and 9.2 for low-, medium-, and high-elevation classes. Latitude interacted with elevation in the 76-mm diameter class, elevation was the main effect in the 152-mm class, but the 228-mm diameter class showed no branchwood volume relation to either latitude or elevation (fig. 1-28).

Live branchwood volume was also positively correlated with crown width (0.86), average live branch diameter (0.78), stembark thickness at 50 percent of tree height (0.73), total volume of stump-root system (0.84), and total stem volume (0.77).

Volume of Live Branchbark (Thousand cm³)

Live branchbark volume was positively correlated with d.b.h., averaging 0.7 (0.39), 3.8 (1.74), and 10.4 (4.43) for the three diameter classes. It was unrelated to latitude, but was inversely correlated with elevation class, particularly in 152-mm trees, as follows:

D.b.h. mm	Elevation class		
	Low	Medium	High
	----- Thousand cm ³ -----		
76	0.8	0.7	0.7
152	4.3	3.8	3.1
228	11.1	10.6	9.5
Average	5.4	5.0	4.4

Volume of live branchbark was also positively correlated with crown width (0.84), crown length (0.56), average live branch diameter (0.70), average ring width at stump height (0.57), lateral rootbark thickness (0.65), stembark thickness at 50 percent of stem height (0.79), total stump-root system volume (0.82), and total stem volume (0.74).

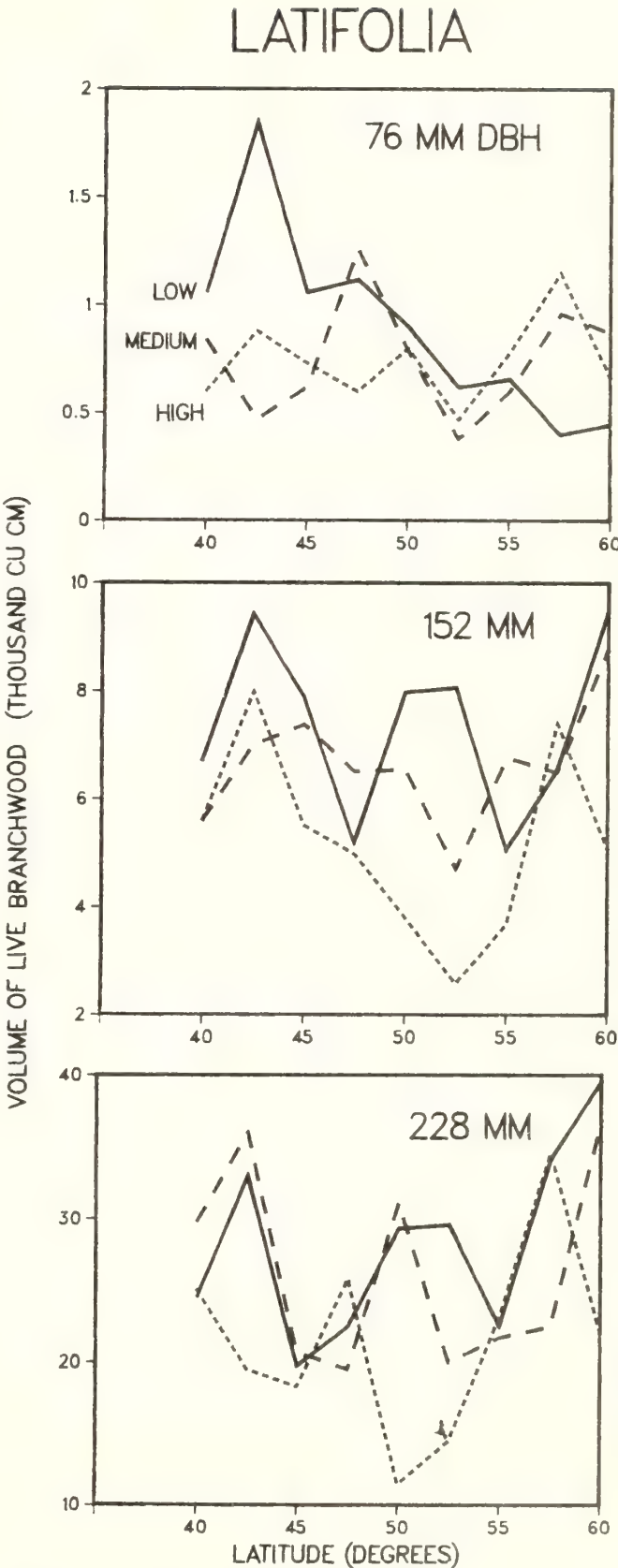


Figure 1-28—Live branchwood volume related to elevational zone and latitude for *latifolia* trees of three diameters.

Volume of Stump-Root System, Wood Plus Bark (Thousand cm³)

Stump-root system volume was positively correlated with tree d.b.h., averaging 4.2 (0.95), 20.9 (3.30), and 49.3 (7.17) for the three diameter classes. For 76-mm trees, system volume was greater in northern than in southern latitudes, and for 228-mm trees, system volumes in southern latitudes were less in lower elevation classes than in higher—except at latitude 57.5 degrees (fig. 1-29).

Volume of the stump-root system including wood and bark was negatively correlated with stembark volume percentage of gross stem volume (-0.71). It was positively correlated with tree height to 25-mm top diameter (0.82), crown width (0.81), number of live branches (0.62), average live branch diameter (0.81), average growth-ring width at stump height (0.57), number of cones on top 25 branches (0.62), stembark thickness at 50 percent of tree height (0.78), total live branch volume (0.84), stem volume including wood and bark (0.95), and complete-tree volume (0.97).

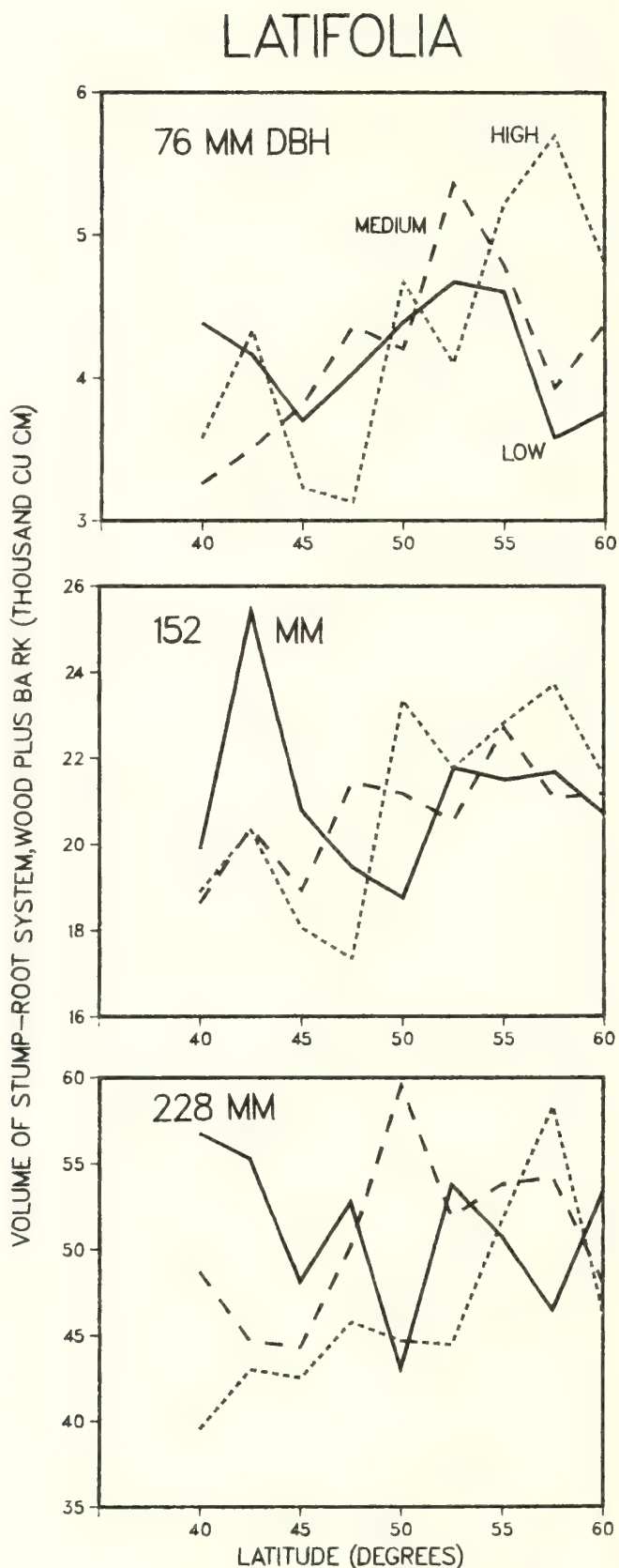


Figure 1-29—Stump-root system volume, wood plus bark, of *latifolia* trees of three diameters related to elevational zone and latitude.

**Volume of Stump, Wood Plus Bark
(Thousand cm³)**

Stump volume (groundline to 152-mm-high stump top) was unrelated to elevational zone, but was positively correlated with tree d.b.h., averaging 1.3 (0.30), 4.2 (1.17), and 8.4 (2.60) for the three diameter classes. Stump volumes were largest in latitudinal zones 40 and 42.5 degrees and smallest between latitudes 52.5 and 60 degrees, depending on d.b.h. (fig. 1-30).

Volume of Lateral Roots, Wood Plus Bark (Thousand cm³)

Lateral root volume (root collar to a radius 305 mm from stump pith) was unrelated to elevational zone, but was positively correlated with tree d.b.h., averaging 1.2 (0.61), 7.5 (2.13), and 17.2 (5.34) for the three diameter classes. Lateral root volumes were smallest or nearly so at latitude 40 degrees and largest at 57.5 or 60 degrees, depending on diameter (fig. 1-31).

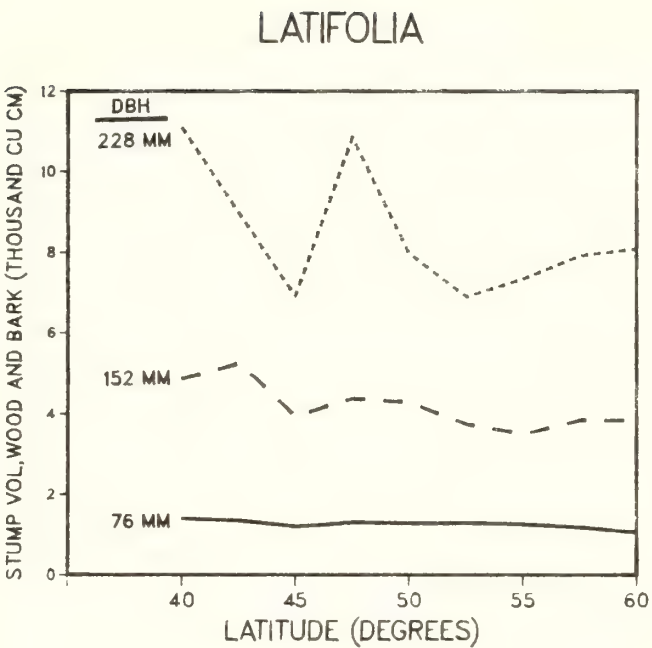


Figure 1-30—Stump volume from groundline to stump top, wood plus bark, related to latitude for *latifolia* trees of three diameters.

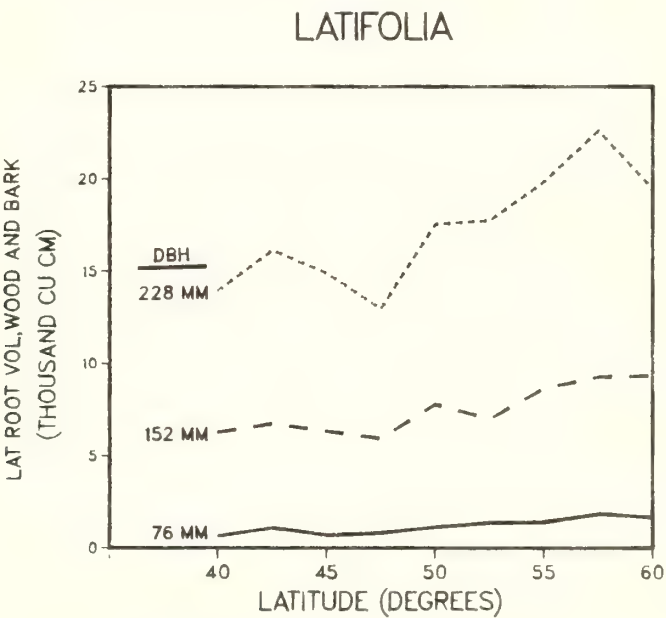


Figure 1-31—Lateral root volume, wood plus bark, related to latitude for *latifolia* trees of three diameters.

Volume of Central Root Mass, Wood Plus Bark (Thousand cm³)

The central root mass shorn of laterals and stump, but with that portion of the taproot recovered by the field crews, had volume positively correlated with tree d.b.h., averaging 1.8 (0.55), 9.3 (2.57), and 23.4 (5.75) for the three diameter classes. For 76-mm trees, volumes were largest in latitudes 50 through 55 degrees and smallest in latitude 57.5 degrees; 152-mm trees had central root mass volume unrelated to either latitude or elevational zone; 228-mm trees had a complex interaction of latitude with elevational zone (fig. 1-32).

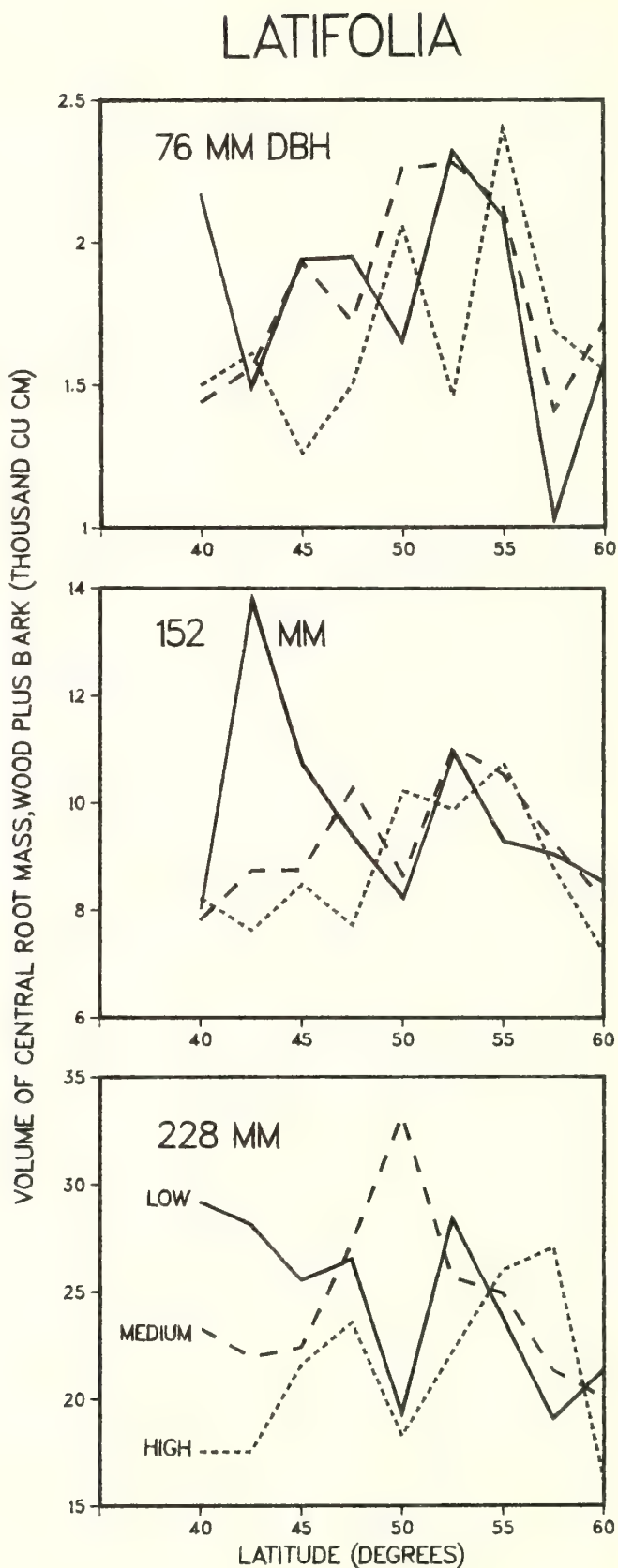


Figure 1-32—Volume of wood plus bark in central root mass including taproot, but shorn of laterals and stump, related to elevational zone and latitude for *latifolia* trees of three diameters.

Volume of Stump-Root System, Wood Only (Thousand cm^3)

The stump-root system wood volume was positively correlated with d.b.h., averaging 3.5 (0.79), 18.1 (3.03), and 44.1 (6.52) for the three diameter classes. For 76-mm trees, wood volumes in root systems were larger in northern latitudes than in southern; elevational trends were absent or complex (fig. 1-33).

The volume of wood in the stump-root system was also positively and closely correlated with total stem volume (0.95) and total tree volume (0.97).

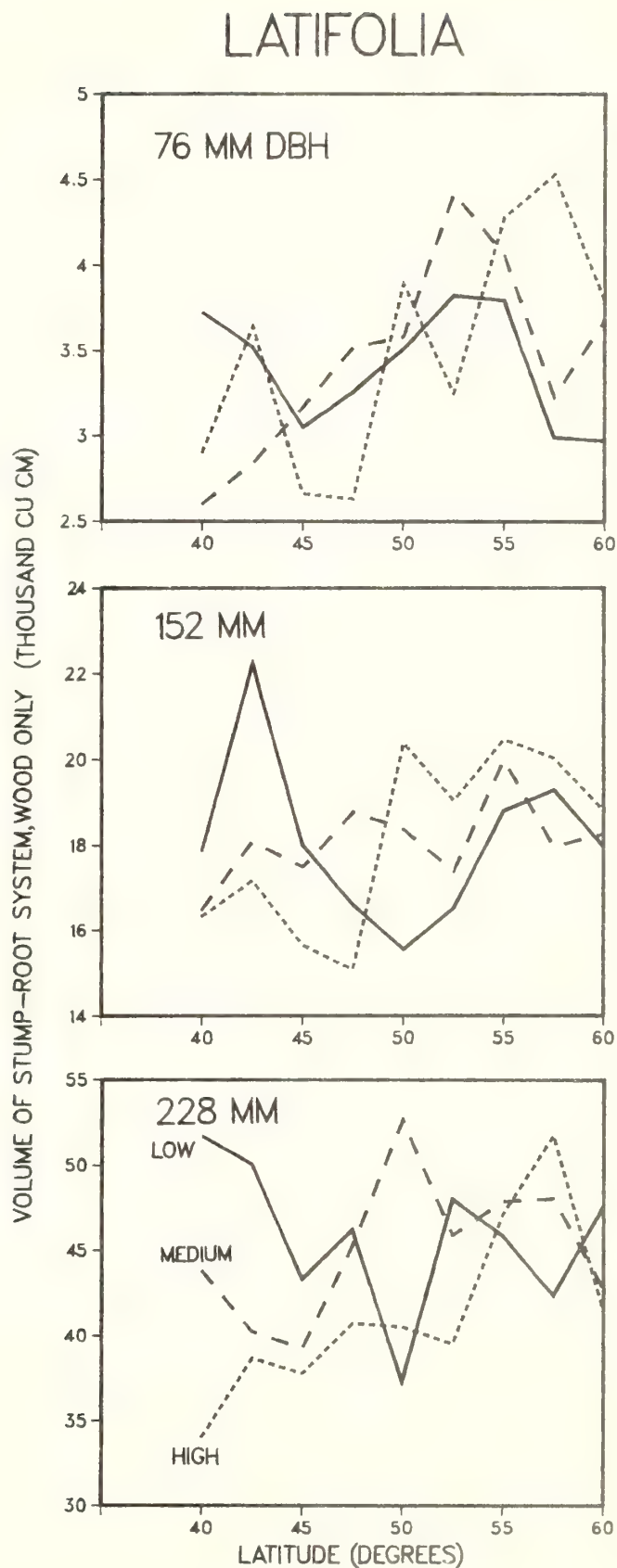


Figure 1-33—Wood volume in stump-root system of *latifolia* trees of three diameters related to elevational zone and latitude.

Volume of Stump, Wood Only (Thousand cm³)

Stumpwood volume was unrelated to elevational zone, but was positively correlated with tree d.b.h., averaging 1.0 (0.26), 3.6 (1.02), and 7.6 (2.50) for the three diameter classes. Trees 152 and 228 mm in d.b.h. had the largest stumpwood volumes in latitudes 40 and 42.5 degrees (fig. 1-34).

Volume of Lateral Roots, Wood Only (Thousand cm³)

Wood volume of lateral roots was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 0.9 (0.50), 6.3 (1.84), and 15.1 (4.50) for the three diameter classes. Volumes were maximum for all three d.b.h. classes in latitudes 57.5 and 60 degrees (fig. 1-35).

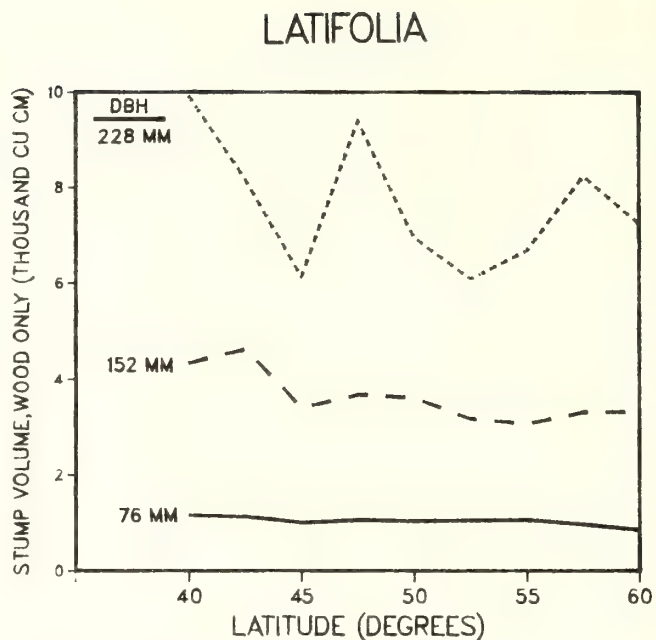


Figure 1-34—Wood volume in stump, groundline to stump top, related to latitude for *latifolia* trees of three diameters.

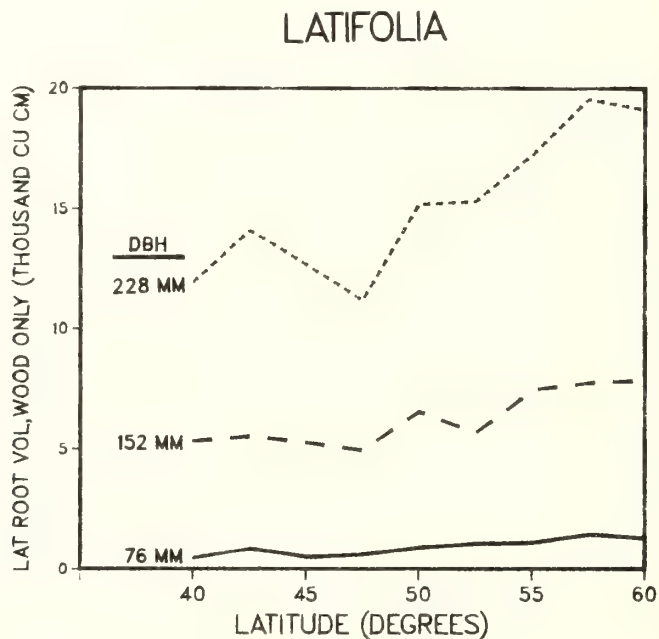


Figure 1-35—Wood volume in lateral roots, root collar to 305-mm radius from tree pith, related to latitude for *latifolia* trees of three diameters.

Volume of Central Root Mass, Wood Only (Thousand cm^3)

Wood volume of the central root mass shorn of stump and laterals, but including taproot, was positively correlated with d.b.h., averaging 1.5 (0.48), 8.3 (2.28), and 21.4 (5.23) for the three diameter classes. For 76-mm trees, volumes were greatest at latitudes 50 through 55 degrees, but were unrelated to elevational zone. Central root mass wood volumes of 152-mm trees were not correlated with elevational zone or latitude. In 228-mm trees were greater in low- and medium-elevation zones than in high zones at all latitudes except 55 and 57.5 degrees, wood volumes were greater in low- and medium-elevation zones than in high zones (fig. 1-36).

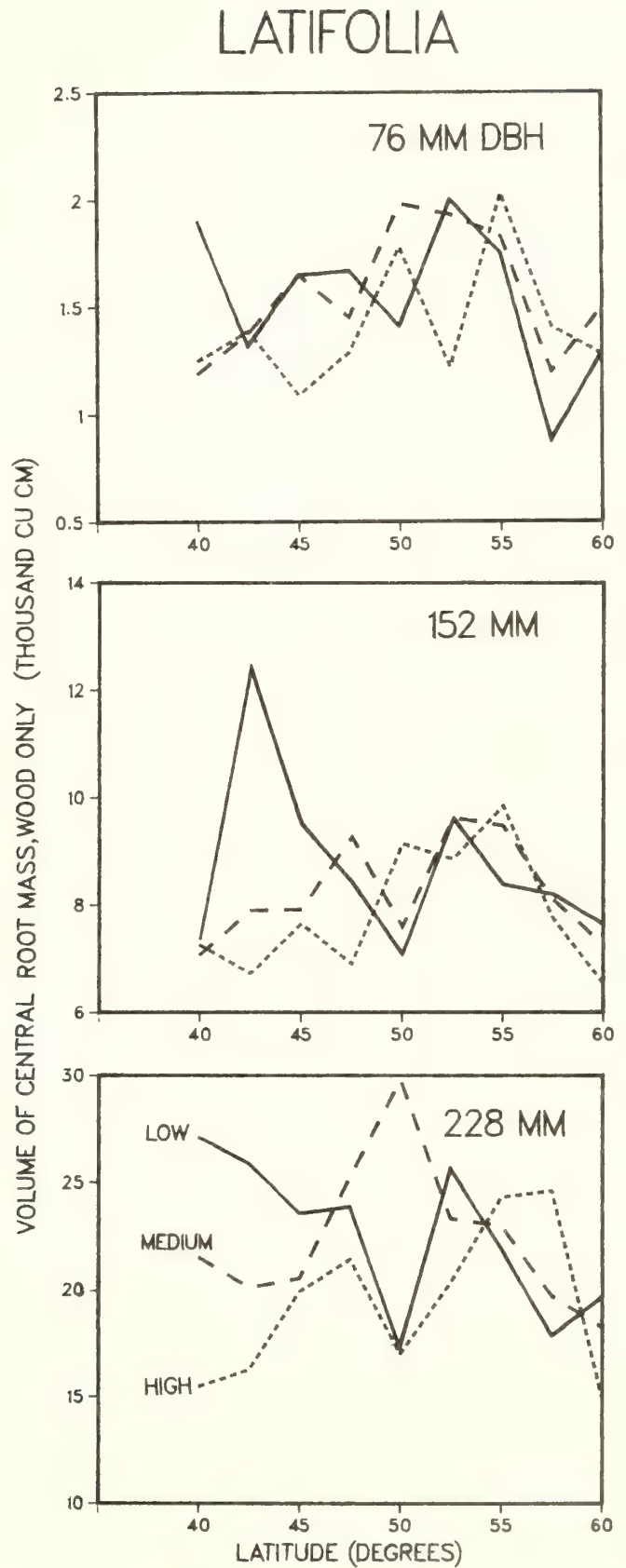


Figure 1-36—Wood volume in central root mass and taproot related to elevational zone and latitude in *latifolia* trees of three diameters.

Volume of Stump-Root System, Bark Only (Thousand cm^3)

Bark volume of the stump-root system was positively correlated with tree d.b.h., averaging 0.8 (0.21), 2.8 (0.68), and 5.3 (1.14) for the three diameter classes. For 76-mm trees, bark volume averaged somewhat more in the five northernmost latitudes than in the four southern latitudes; in the three northernmost latitudes, trees in high-elevation zones had more bark volume than those in low or medium zones (fig. 1-37). For the 152- and 228-mm trees, no elevational or latitudinal trends were discernible.

The volume of bark in the stump-root system was positively correlated with the volume of live branchwood (0.80) and bark (0.79), with the volume of stemwood (0.87) and bark (0.91), and with the volume of treewood (0.89) and bark (0.93).

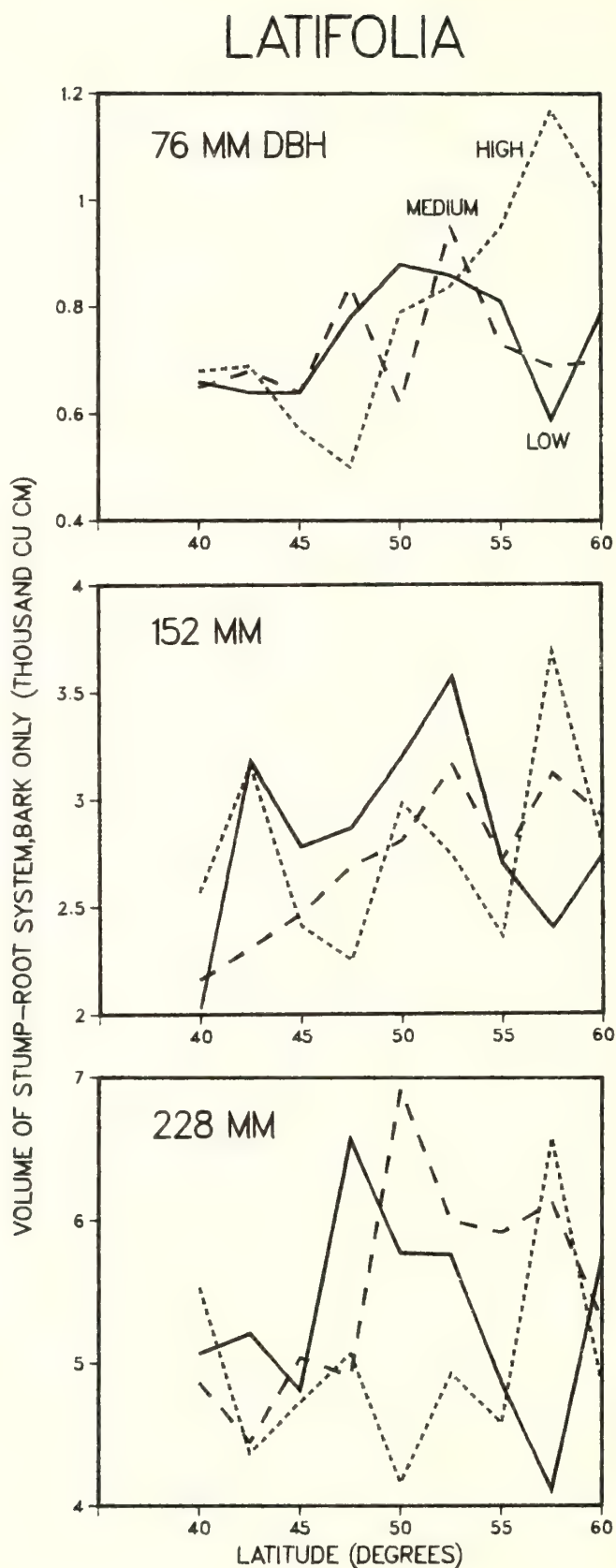


Figure 1-37—Bark volume in stump-root system related to elevational zone and latitude for *latifolia* trees of three diameters.

Volume of Stump, Bark Only (Thousand cm³)

Bark volume from stump top to ground level was positively correlated with d.b.h., averaging 0.21 (0.08), 0.56 (0.26), and 0.92 (0.42) for the three diameter classes. For 76-mm trees, bark volume was greatest at 47.5 degrees latitude in low-elevation trees; in 152-mm trees latitude and elevational classes were unrelated to stump-bark volume; in 228-mm trees, however, volume of stump-bark diminished from 40 through 45 degrees latitude, showed a sharp increase at 47.5 degrees, and then diminished in more northerly latitudes (fig. 1-38).

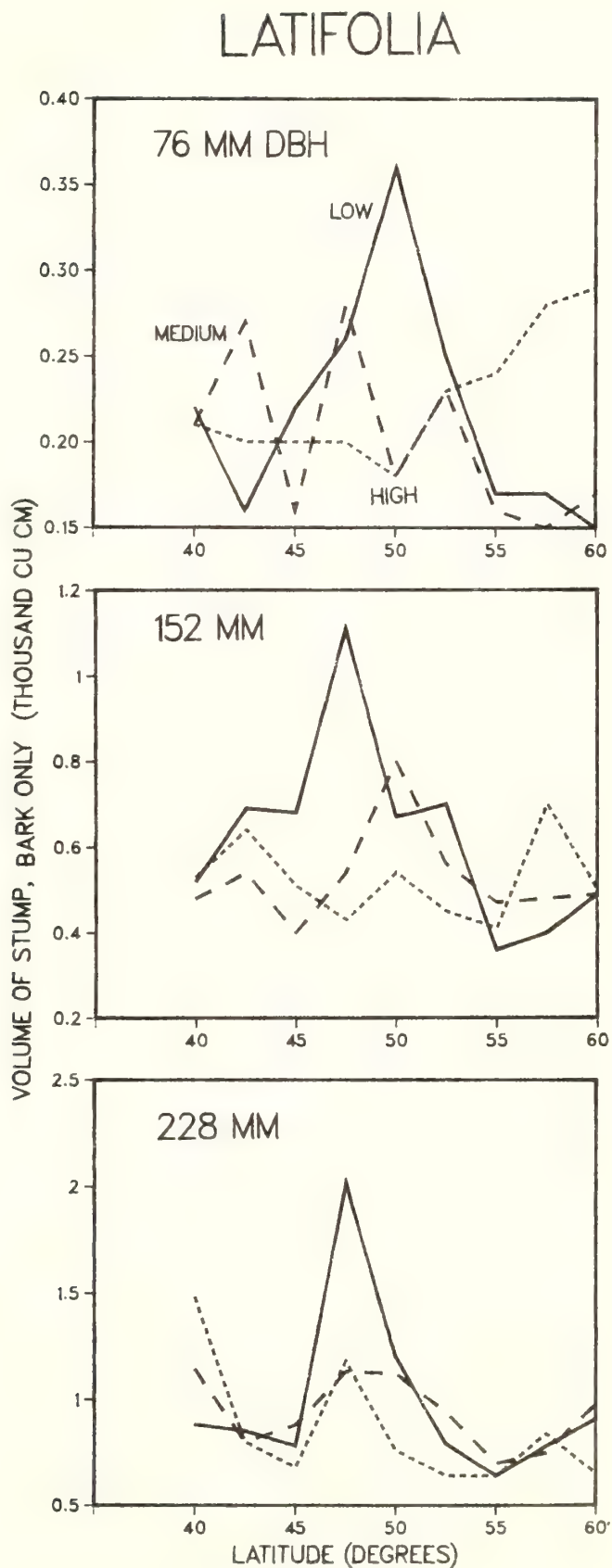


Figure 1-38—Bark volume of stump related to elevational zone and latitude for *latifolia* trees of three diameters.

Volume of Lateral Roots, Bark Only (Thousand cm^3)

Bark volume of lateral roots from root collar to a radius of 305 mm from stump pith was positively correlated with d.b.h., averaging 0.28 (0.13), 1.22 (0.39), and 2.37 (0.83) for the three diameter classes. In all three diameter classes, volume of lateral rootbark generally increased with increasing latitude, but the relationship of elevation class to volume was more complex (fig. 1-39). The average for the four southern latitudes was 1.08; that for the five northern latitudes was 1.45.

Volume of Central Root Mass, Bark Only (Thousand cm^3)

Volume of bark on the central root mass, including taproot, was unrelated to elevational or latitudinal zones, but was positively correlated with d.b.h., averaging 0.26 (0.93), 0.99 (0.38), and 2.00 (0.79) for the three diameter classes.

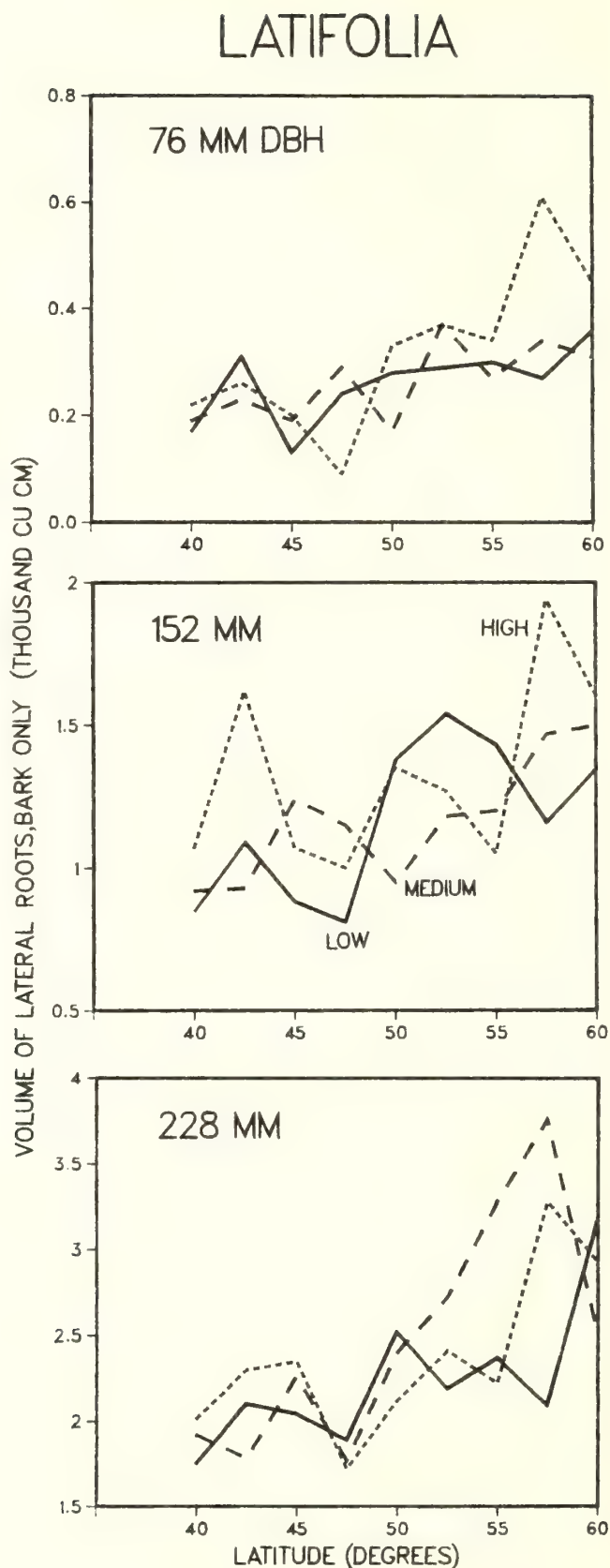


Figure 1-39—Bark volume of lateral roots related to elevational zone and latitude for *latifolia* trees of three diameters.

Stem Volume to Apical Tip, Wood Plus Bark (Thousand cm³)

Total stem volume averaged 24.8 (5.5), 156.6 (31.4), and 413.9 (76.1) for the three diameter classes. Trees in high-elevation zones had less stem volume than those in lower zones, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
	----- Thousand cm ³ -----		
76	25.1	25.1	24.2
152	155.3	163.2	151.2
228	432.1	418.4	391.2
Average	204.2	202.3	188.9

Northern-latitude 76-mm trees averaged more total volume than southern. Trees 152 mm had the largest volumes in latitude zones 50 through 55 degrees and smallest volumes in the three southernmost latitudes. Trees in the 228-mm class also had largest volumes in latitude zones 50 through 55 degrees, but had smallest volumes in the 40- and 57.5-degree latitudinal zones (fig. 1-40).

Stem volume to apical tip, including wood and bark, was positively correlated with d.b.h. (0.94), tree height (0.89), length of taproot (0.61), crown width (0.74), average live branch diameter (0.77), stembark thickness at 50 percent of tree height (0.74), total live branch volume (0.77), and total volume of stump-root system (0.95).

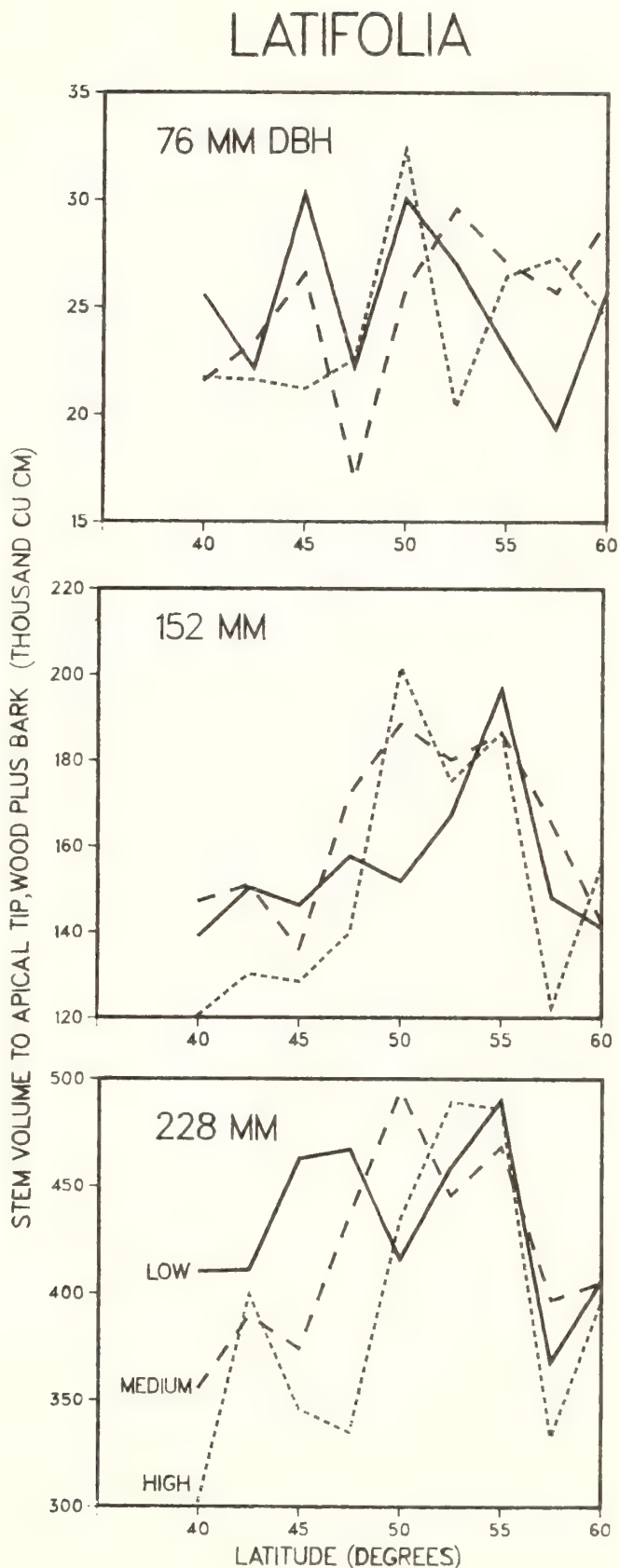


Figure 1-40—Stem volume from stump top to apical tip, wood plus bark, related to elevational zone and latitude for *latifolia* trees of three diameters.

Stemwood Volume to the Apical Tip (Thousand cm³)

Stemwood volume to the apical tip for the three diameter classes averaged 21.2 (5.0), 140.3 (29.2), and 377.4 (71.2). Except for medium-elevation 76- and 152-mm trees, stemwood volume to apical tip was negatively correlated with elevation zone, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
	----- Thousand cm ³ -----		
76	21.5	21.6	20.6
152	138.4	146.4	136.2
228	394.3	380.9	357.0
Average	184.8	183.0	171.3

Stemwood volume was least or nearly so at 40 degrees (for 76-mm trees the least was at 47.5 degrees), and averaged most at 50 degrees for 76-mm trees and 55 degrees for the two larger diameter classes (fig. 1-41). Stemwood volume was positively and equally correlated to the same factors as noted for total stem volume; it was also closely correlated to stembark volume (0.96).

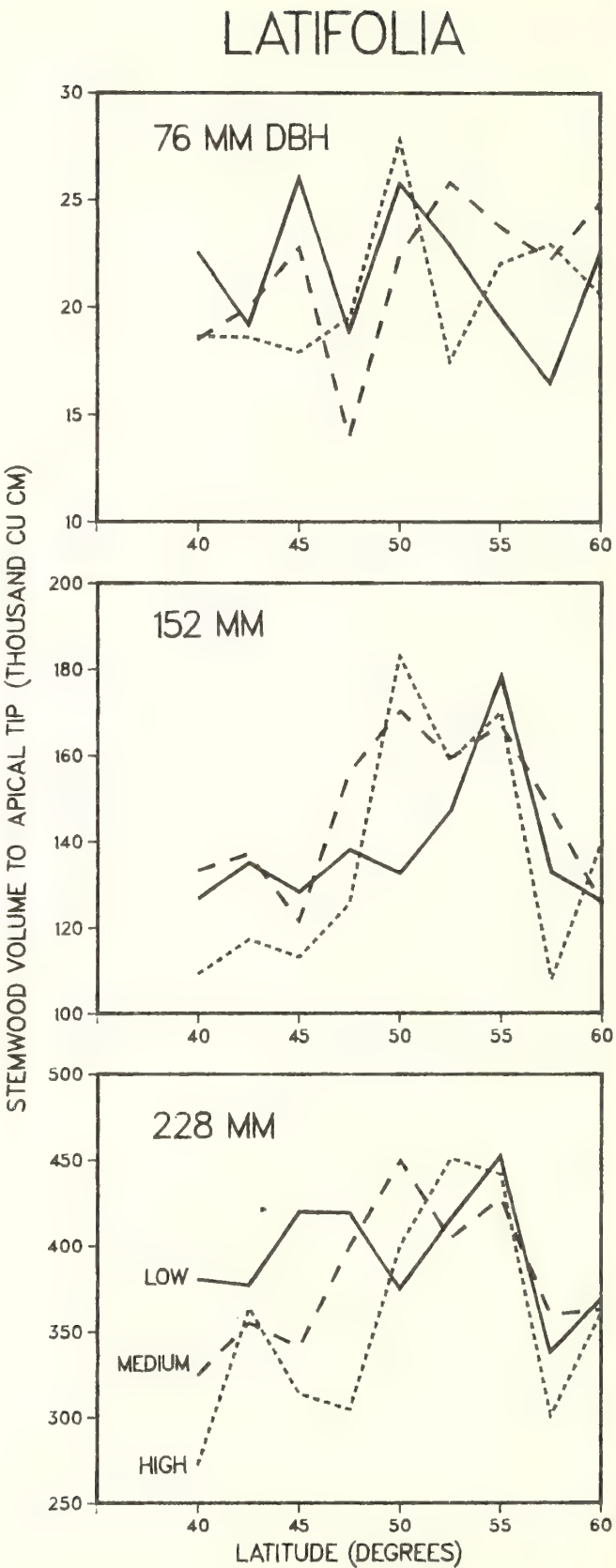


Figure 1-41—Stemwood volume from stump top to apical tip in *latifolia* trees of three diameters related to elevational zone and latitude.

Stembark Volume to Apical Tip (Thousand cm³)

Stembark volume to apical tip for the three diameter classes averaged 3.6 (0.70), 16.3 (0.44), and 36.5 (7.31). In the six southern latitudinal zones stembark volume averaged less in high-elevation than in low-elevation zones, but in the three northernmost zones the reverse was true. For all diameter classes, stembark volume was lowest at 40 degrees latitude; highest averages or nearly so were in latitudinal zones 50 through 55 degrees (fig. 1-42).

Stembark volume was positively and about equally correlated to the same factors as noted for total stem volume. Stembark thickness at 50 percent of tree height is a better measurable indicator of stembark volume ($r = 0.82$) than stumpbark thickness ($r = 0.64$).

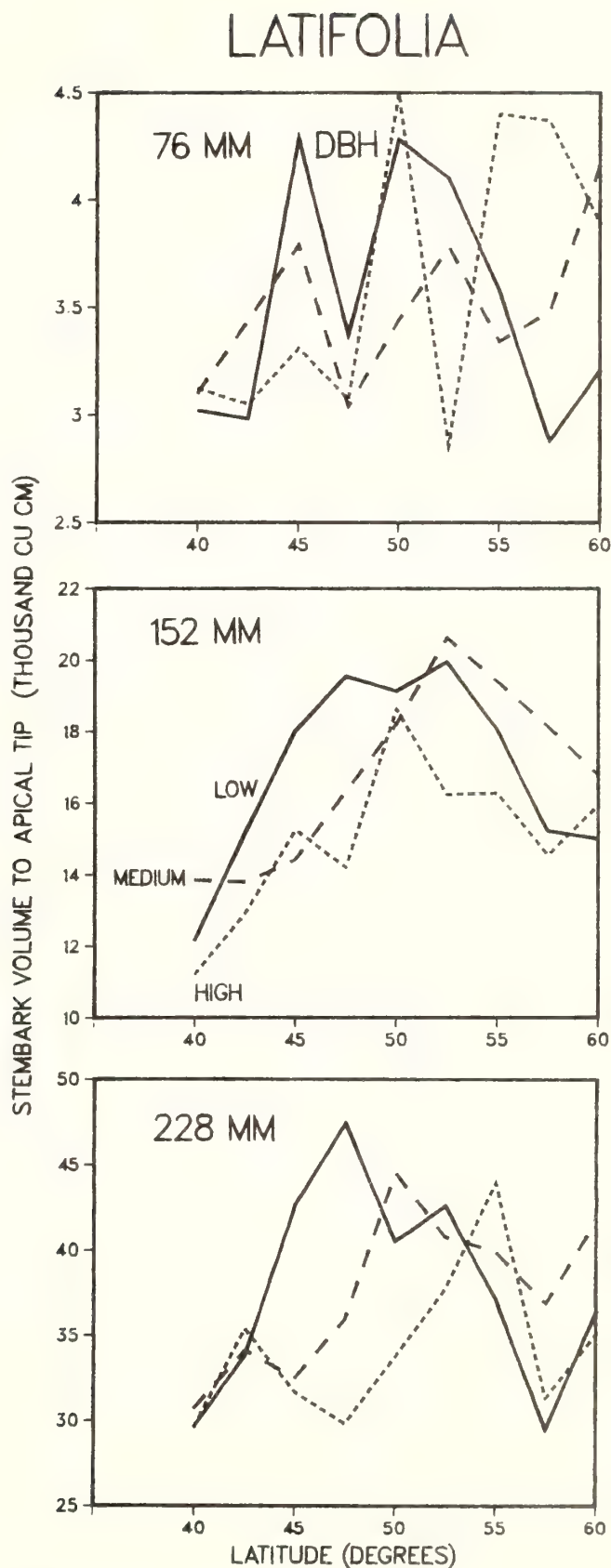


Figure 1-42—Stembark volume from stump top to apical tip in *latifolia* trees of three diameters related to elevational zone and latitude.

Complete-Tree Volume, Wood Plus Bark (Thousand cm³)

Complete-tree volume of wood plus bark (stump-root system, stem, live and dead branches—but not foliage) averaged 31.0 (5.6), 191.1 (32.1), and 509.0 (75.6) for the three diameter classes. Complete trees in high-elevation zones had least volume and, except for 152-mm trees, those in low-elevation zones had most volume, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
	----- Thousand cm ³ -----		
76	31.6	31.2	30.3
152	192.6	197.6	183.0
228	535.6	516.0	475.3
Average	253.3	248.3	229.6

Average complete-tree volumes were lowest at 40 degrees for 152- and 228-mm trees, and nearly so for 76-mm trees; largest average volumes were at 50 degrees for 76-mm trees and at 55 degrees for trees of the two larger diameter classes. In general, complete-tree volume averages were largest in latitude zones 50 through 55 degrees (fig. 1-43).

Complete-tree volume, including wood and bark, was closely correlated with d.b.h. (0.96) and total volume of the stump-root system (0.97). It was also positively correlated with tree height (0.87), live branch volume (0.82), average diameter of live branches (0.79), crown width (0.78), and stem bark thickness at 50 percent of stem height (0.76). Crown length had weaker correlation (0.54).

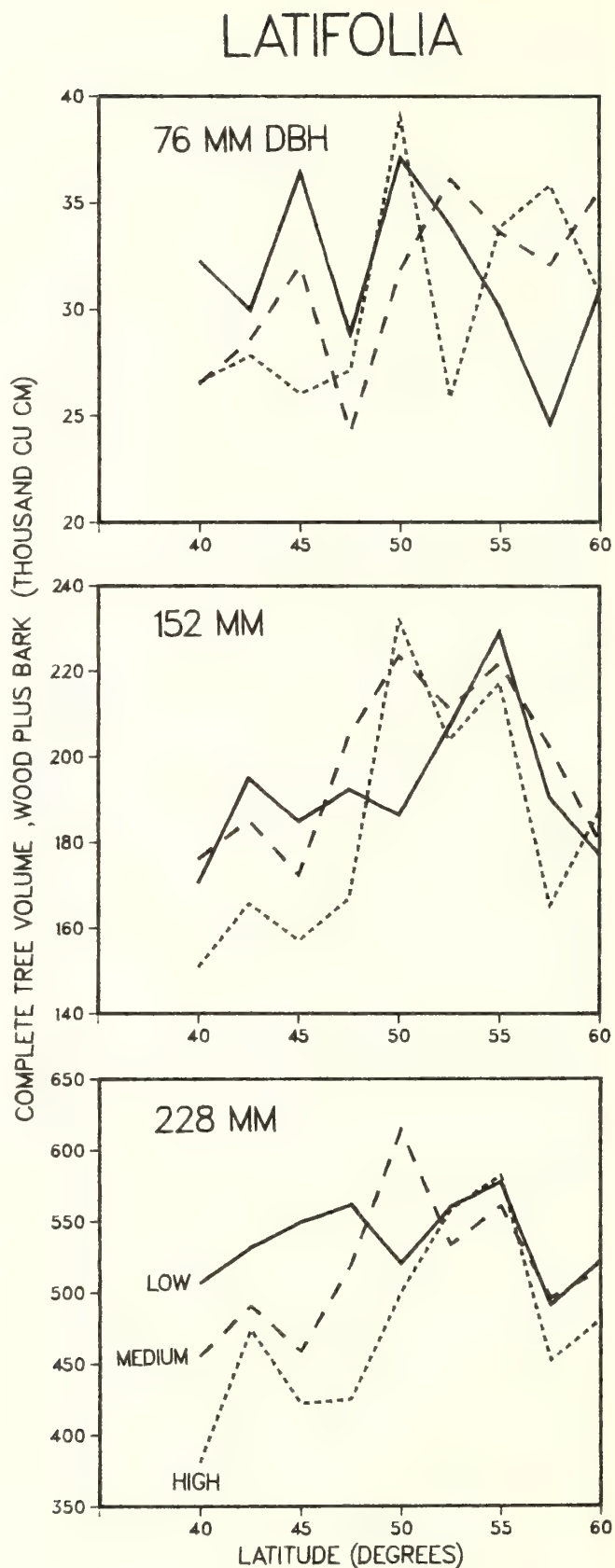


Figure 1-43—Complete-tree volume, wood plus bark, in *latifolia* trees of three diameters related to elevational zone and latitude.

Complete-Tree Volume, Wood Only (Thousand cm³)

Complete-tree volume of wood averaged 26.0 (5.1), 168.5 (30.6), and 456.8 (71.4) for the three diameter classes. Trees from high-elevation zones had least wood volume and, with the exception of the 152-mm trees, those from low zones had the most wood volume, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
	----- Thousand cm ³ -----		
76	26.6	26.3	25.2
152	169.3	174.2	162.1
228	481.4	462.4	426.6
Average	225.8	221.0	204.5

Complete-tree wood volume averaged maximum for all three diameter classes in latitude zones 50 through 55 degrees and minimum for 152- and 228-mm trees in the 40-degree zone; 76-mm trees had minimum wood volume at 47.5 degrees (fig. 1-44).

Complete-tree wood volume was positively and equally correlated with the same characteristics noted for wood-plus-bark complete-tree volume.

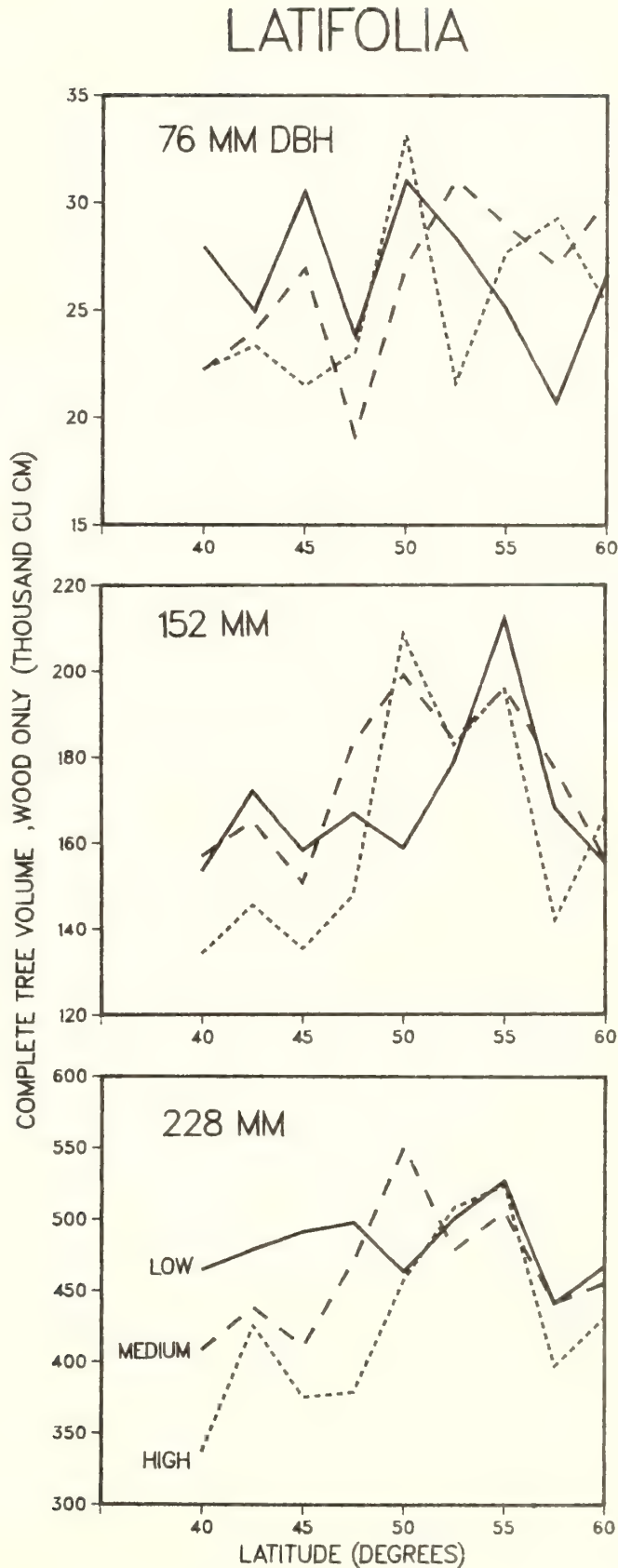


Figure 1-44—Complete-tree volume of wood only in *latifolia* trees of three diameters related to elevational zone and latitude.

Complete-Tree Volume, Bark Only (Thousand cm³)

Bark volume of complete trees averaged 5.0 (0.91), 22.8 (4.22), and 52.2 (9.01) for the three diameter classes. For 152- and 228-mm trees, complete-tree bark volume varied inversely with elevational zone; bark volume on 76-mm trees was unrelated to elevational zone, as follows:

D.b.h. mm	Elevation zone		
	Low	Medium	High
76	5.0	4.9	5.1
152	24.1	23.4	20.9
228	54.2	53.6	48.7
Average	27.8	27.3	24.9

Complete-tree bark volume averages for all three diameter classes were smallest in the 40-degree latitude zone. Trees 76 mm had highest bark volume at 50 degrees (5.6), 152 mm at 52.5 degrees (25.6), and 228 mm at 52.5 and 55 degrees (54.7) (fig. 1-45).

Complete-tree bark volume was positively and equally correlated with the same characteristics noted for wood-plus-bark complete-tree volume, except that correlations were closer with stem bark thickness at 50 percent of tree height (0.85) and with total live branch volume (0.88).

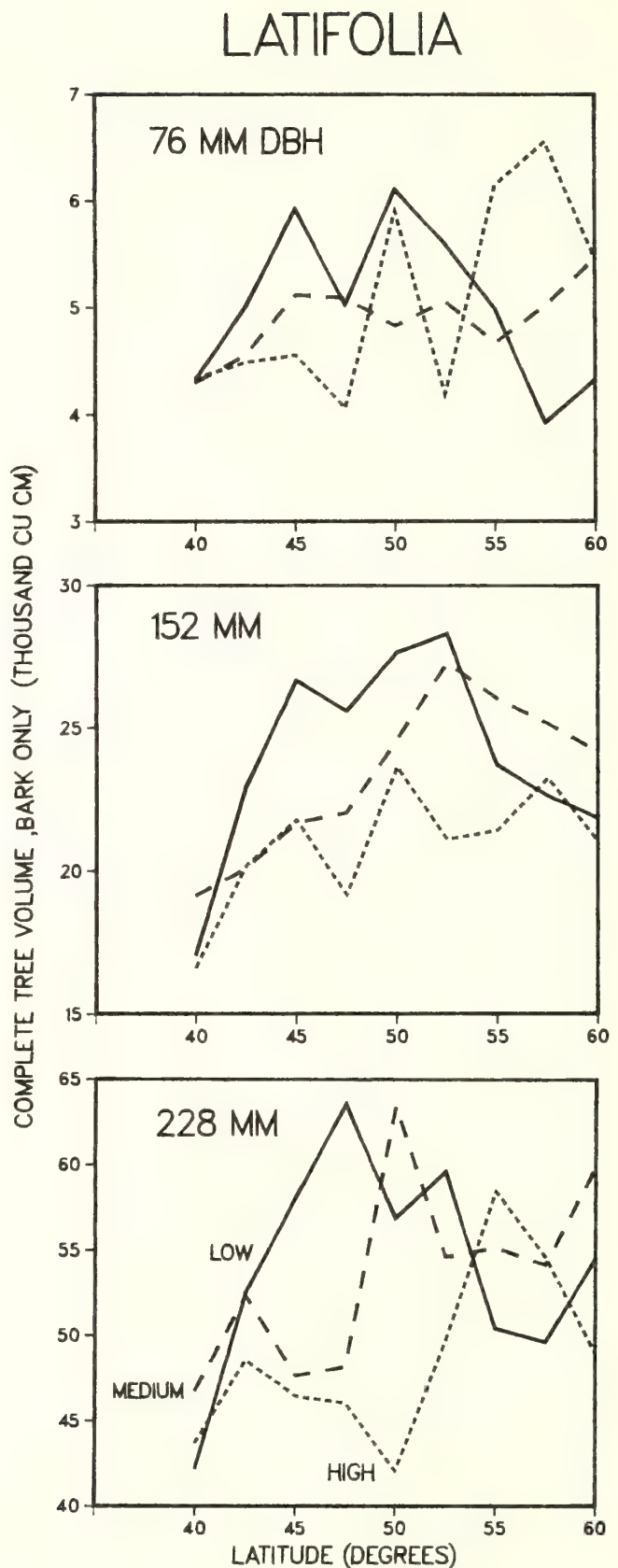


Figure 1-45—Complete-tree volume of bark only in *latifolia* trees of three diameters related to elevational zone and latitude.

Stembark as Percentage of Gross Stem Volume by Height in Tree

Stembark percentage at various heights in the trees was unrelated to elevational zone, except at stump height. Low-elevation-zone trees at latitudes 45, 47.5, 50, and 52.5 degrees had bark percentages significantly above the 12.1 percent mean for stump height, averaging 13.4, 19.2, 18.1, and 15.9 percent, respectively.

Bark percentage was related to latitude only at 50, 60, and 90 percent of tree height, where—at 45 degrees latitude only—bark volume percentage was one to two percentage points above the means for these heights.

The dominant factors were tree d.b.h. and height in tree. In all three diameter classes, bark percentage was relatively large at stump height, diminished from stump height to 10 or 20 percent of tree height, and then was positively correlated with height in tree (fig. 1-46).

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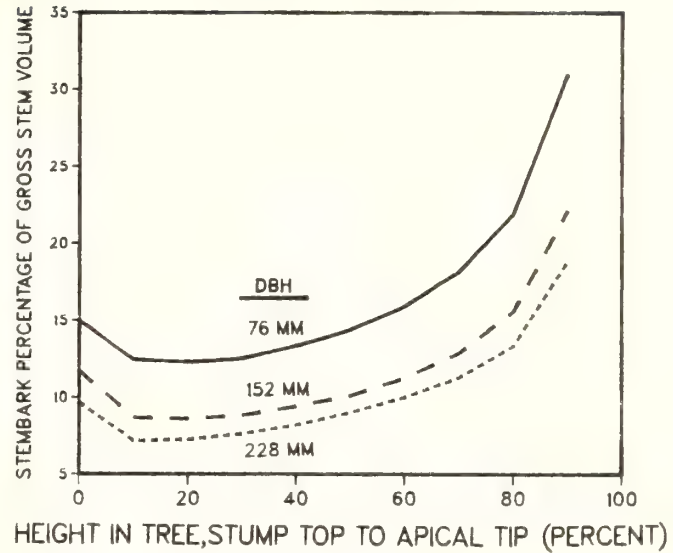


Figure 1-46—Stembark percentage of gross stem volume related to height in *latifolia* trees of three diameters; latitudinal and elevational data pooled.

Stembark as Percentage of Gross Stem Volume

Stembark volume as a percentage of gross volume of stem from stump top to apical tip was inversely correlated with d.b.h., averaging 14.6 (2.2), 10.5 (1.8), and 8.9 (1.3) percent for the three diameter classes; that is, small trees have a higher percentage of stembark than large trees. Low-elevation zones had trees with greatest stembark percentages in latitudinal zones 47.5 and 50 degrees, with minimum percentage in the 40-degree zone. Medium-elevation zones had trees with greatest stembark percentages at the northernmost latitude, and least at latitudes 50 and 55 degrees. High-elevation zones had trees with greatest stembark percentages at 57.5 degrees and least at 50 degrees. For all diameter classes, latitude interacted with elevational zone (fig. 1-47).

Stembark percentage of total stem volume to apical tip was most closely correlated—negatively—with tree height (-0.81), d.b.h. (-0.77), and length of stem below crown (-0.67).

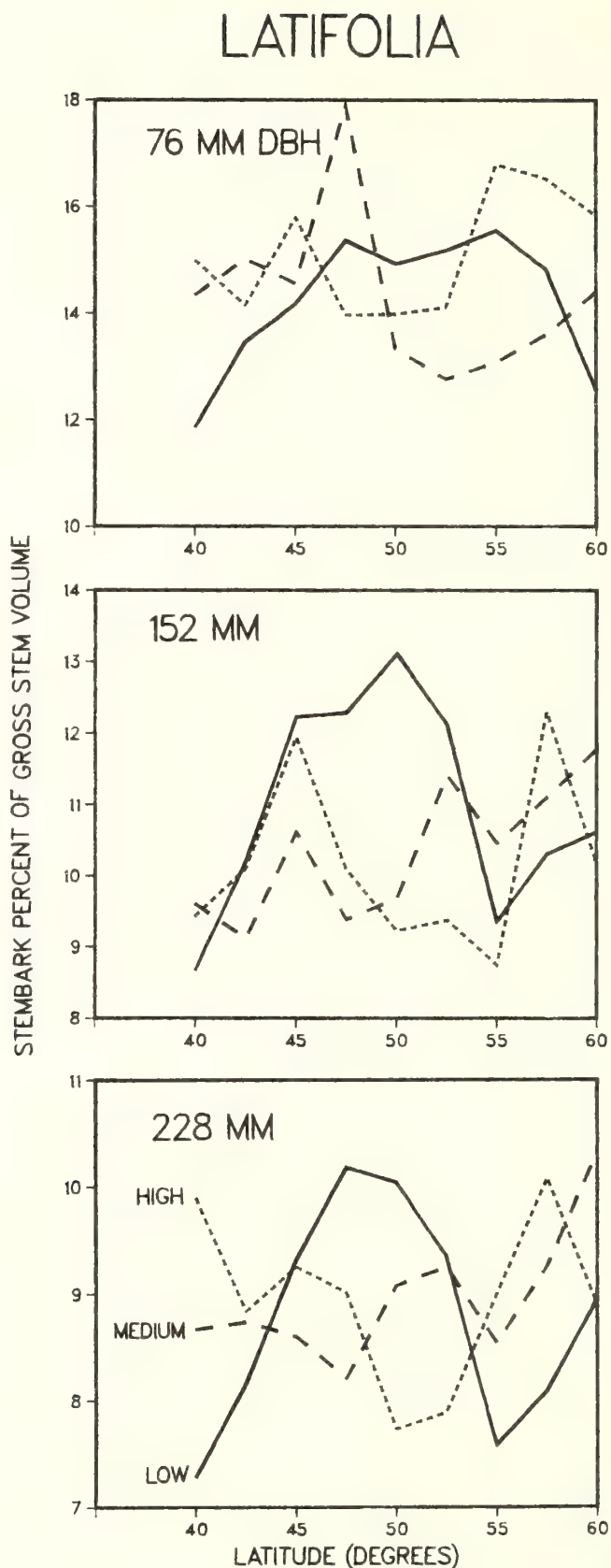


Figure 1-47—Stembark percentage of gross stem volume related to elevational zone and latitude for *latifolia* trees of three diameters.

Stump-Rootbark as Percentage of Gross Stump-Root System Volume

Stump-rootbark volume as a percentage of gross volume of stump-root system was unrelated to elevation, but, as in stems, was inversely correlated with tree d.b.h., averaging 17.9 (3.3), 13.3 (2.6), and 10.7 (1.9) percent bark for 76-, 152-, and 228-mm diameter classes, respectively.

Bark volume percentage in the stump-root system was unrelated to latitude except for the 152-mm diameter class where percentage of bark volume was greatest in latitudinal zones 50 and 52.5 degrees and least at latitude 40 degrees (fig. 1-48).

Stump-rootbark volume percentage of total stump-root system volume was most closely correlated—negatively—with d.b.h. and tree height ($r = -0.74$ for each).

Live Branchbark as Percentage of Gross Live Branch Volume

Branchbark volume percentage of gross live branch volume was unrelated to elevational zone, but was inversely correlated with tree d.b.h., averaging 46.8 (5.9), 37.1 (5.5), and 29.4 (5.3) percent for the 76-, 152-, and 228-mm diameter classes.

Latitude was related to branchbark volume percentage in all three tree diameter classes (fig. 1-49); this percentage was least in the most southerly and in the most northerly zones—40 and 60 degrees—and maximum in intermediate zones. For 76-mm trees, branchbark volume percentage was greatest in latitudinal zones 52.5 and 55 degrees; for 152- and 228-mm trees, at 47.5 degrees.

Live branchbark percentage of total live branch volume was negatively correlated with average branch diameter (-0.82), d.b.h. (-0.79), total volume of stump-root system (-0.77), total stem volume (-0.75), tree height (-0.69), and crown width (-0.69).

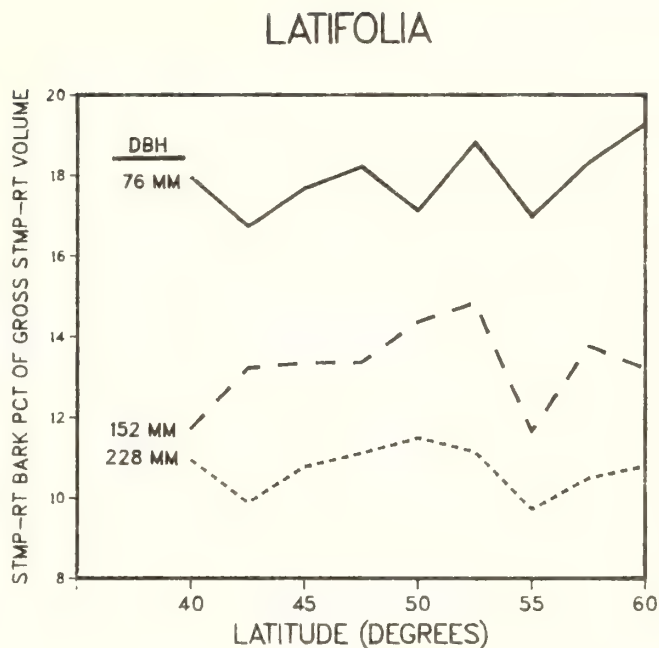


Figure 1-48—Bark volume of stump-root system as a percentage of gross stump-root system volume related to latitude for *latifolia* trees of three diameters.

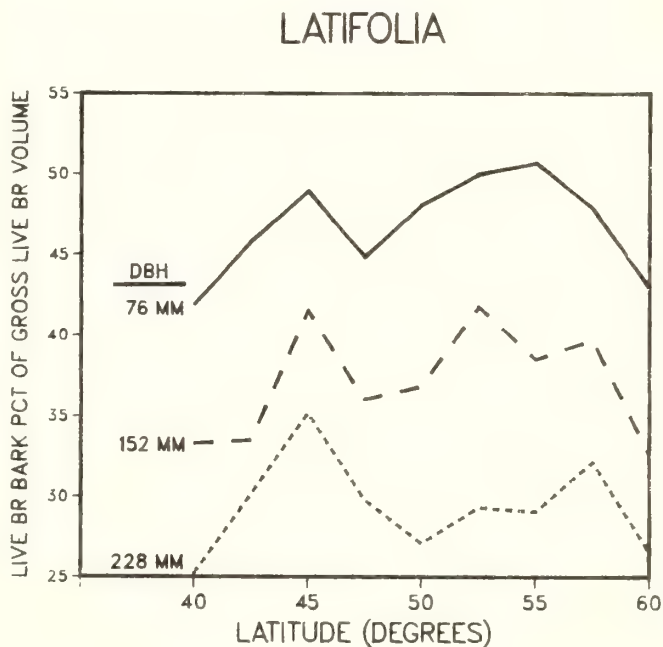


Figure 1-49—Bark volume of live branches as a percentage of gross live branch volume related to latitude for *latifolia* trees of three diameters.

Bark of Complete Tree as Percentage of Complete-Tree Volume

Complete-tree bark volume as a percentage of complete-tree volume was inversely correlated with d.b.h., averaging 16.3 (2.7), 12.1 (2.1), and 10.4 (1.7) percent for 76-, 152-, and 228-mm trees.

The latitude-elevation interaction was complex, permitting no generalization (fig. 1-50).

Bark volume percentage of complete-tree volume was positively correlated with stembark percentage of the wood-plus-bark volume at 50 percent of tree height (0.93) and negatively correlated with tree height (-0.83), d.b.h. (-0.73), and total stump-root system volume (-0.68).

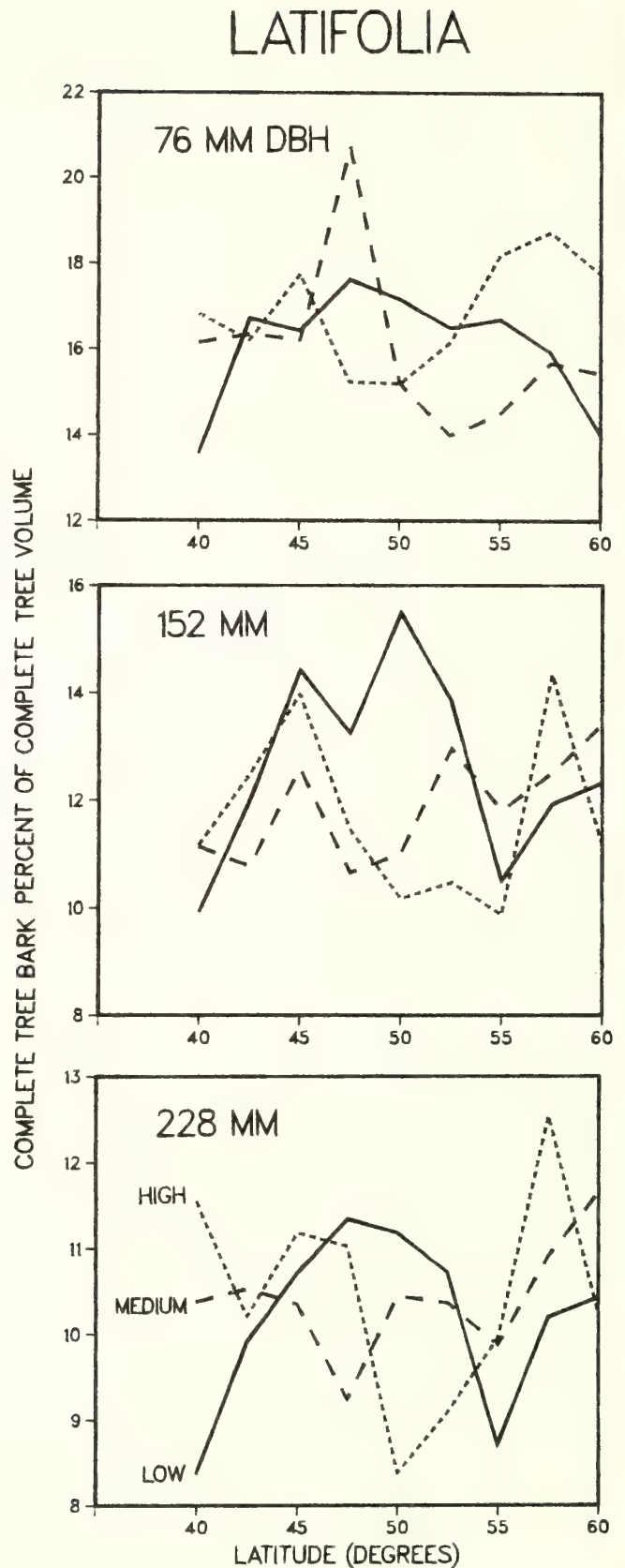


Figure 1-50—Bark volume of complete tree as a percentage of gross volume of complete tree related to elevational zone and latitude for *latifolia* trees of three diameters.

Stemwood as Percentage of Complete-Tree Wood Volume

Stemwood volume averaged 82.1 percent of complete-tree wood volume; this percentage was unrelated to elevational zone; however, it varied slightly—but significantly—with d.b.h., averaging 81.1 (4.9), 82.9 (4.1), and 82.3 (4.8) percent for 76-, 152-, and 228-mm trees.

Volume of stemwood as a percentage of treewood also varied significantly with latitude; it averaged largest at 52.5 degrees (84.0 percent) and smallest at 57.5 degrees, where it was 78.7 percent (fig. 1-51).

Volume of stemwood as a percentage of complete-tree wood volume was poorly correlated with the characteristics measured; it had closest correlation—positive—with tree height (0.46) and length of stem below crown (0.54).

Live Branchwood as Percentage of Complete-Tree Wood Volume

Live branchwood averaged 4.3 percent of complete-tree wood volume; as with stemwood, this percentage was unrelated to elevational zone but did vary significantly with d.b.h., averaging 3.2 (2.03), 4.0 (1.95), and 5.7 (2.81) percent for 76-, 152-, and 228-mm trees.

Live branchwood as a percentage of treewood volume also varied significantly with latitude; with diameter data pooled averages were lowest at 52.5 degrees (3.0 percent) and highest (4.8 to 5.4 percent) in the two southernmost and two northernmost latitudinal zones (fig. 1-52).

Live branchwood as a percentage of complete-tree volume was positively correlated with crown width (0.64), average live branch diameter (0.52), and crown ratio (0.42).

LATIFOLIA

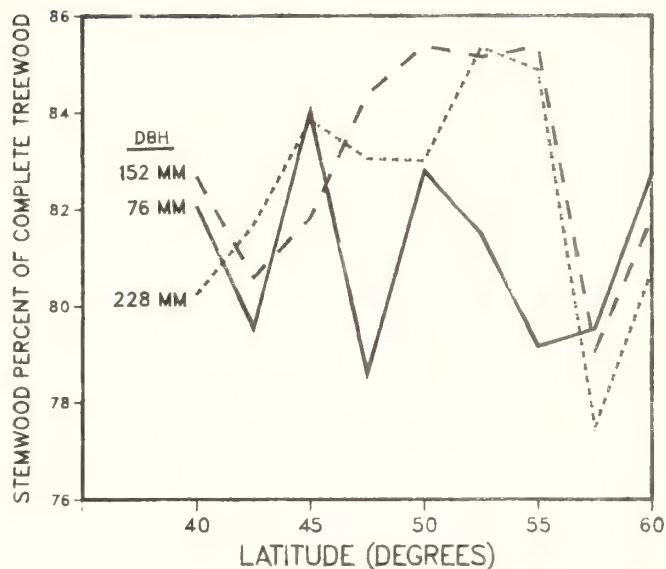


Figure 1-51—Stemwood as a percentage of complete-tree wood volume related to latitude for *latifolia* trees of three diameters.

LATIFOLIA

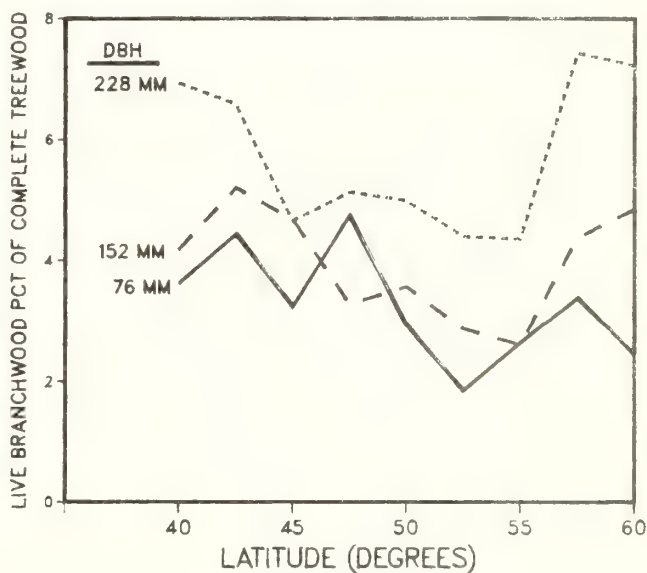


Figure 1-52—Live branchwood as a percentage of complete-tree wood volume related to latitude for *latifolia* trees of three diameters.

Dead Branchwood as Percentage of Complete-Tree Wood Volume

Dead branchwood volume averaged 2.1 percent of complete-tree wood volume, with standard deviation of 1.82; unlike live branchwood, this percentage was unrelated to d.b.h., but did vary inversely with elevational zone, averaging 2.8, 2.0, and 1.7 percent for low, medium, and high zones, respectively.

Dead branchwood percentage of tree volume also varied significantly with latitude; with diameter data pooled averages were lowest (1.6 percent) at 40 degrees and, for reasons not clear, averages more than doubled (4.0 percent) in the 57.5 percent latitudinal zone (fig. 1-53).

Dead branchwood volume percentage of complete-tree wood was poorly correlated with tree characteristics, except for negative correlation with stemwood percentage of treewood volume (-0.52) and positive correlation with dead branchwood volume (0.66).

Stumpwood as Percentage of Complete-Tree Wood Volume

From groundline to stump top, stumpwood averaged 2.7 percent of complete-tree volume; this percentage was unrelated to elevational zone but varied inversely with d.b.h., averaging 4.1 (1.27), 2.2 (0.74), and 1.7 (0.71) percent for 76-, 152-, and 228-mm trees, respectively.

Stumpwood percentage of treewood volume also varied significantly with latitude for all three diameter classes (fig. 1-54); with diameter data pooled, stumpwood percentage of treewood volume averaged 3.3 percent for the two most southerly latitudes and 2.5 percent for the seven northern latitudes.

Stumpwood volume percentage of complete-tree wood was negatively correlated with tree height (-0.80), d.b.h. (-0.70), total stem volume (-0.69), and stem length below crown (-0.68).

Stump-Root System Wood as Percentage of Complete-Tree Wood Volume

Total stump-root system wood (stump, central root collar and taproot, and laterals to 305 mm radius from stump pith) averaged 11.5 percent of complete-tree wood volume. The percentage was unrelated to elevational or latitudinal zone, but was inversely correlated with d.b.h., averaging 13.6 (3.25), 10.9 (1.84), and 9.8 (1.73) percent for 76-, 152-, and 228-mm trees, respectively.

Stump-root system wood volume as a percentage of complete-tree wood volume was positively correlated with stembark percentage of gross stem volume (0.65) and negatively correlated with tree height (-0.73), stem length below crown (-0.66), and, as noted above, with d.b.h. (-0.54).

LATIFOLIA

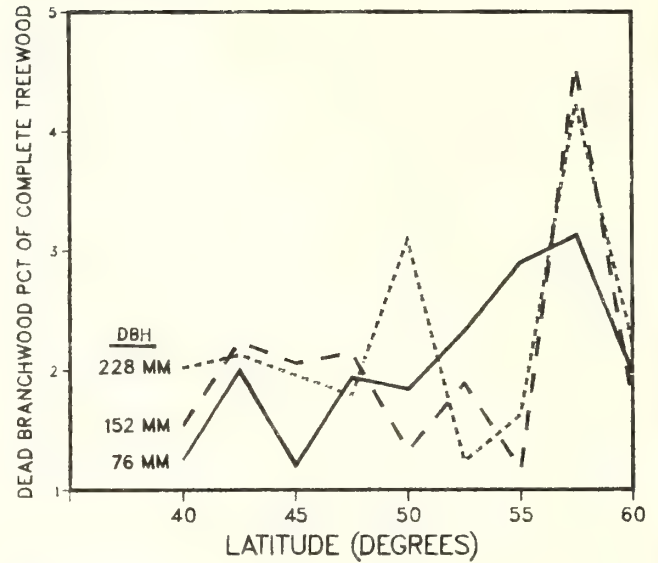


Figure 1-53—Dead branchwood as a percentage of complete-tree wood volume related to latitude for *latifolia* trees of three diameters.

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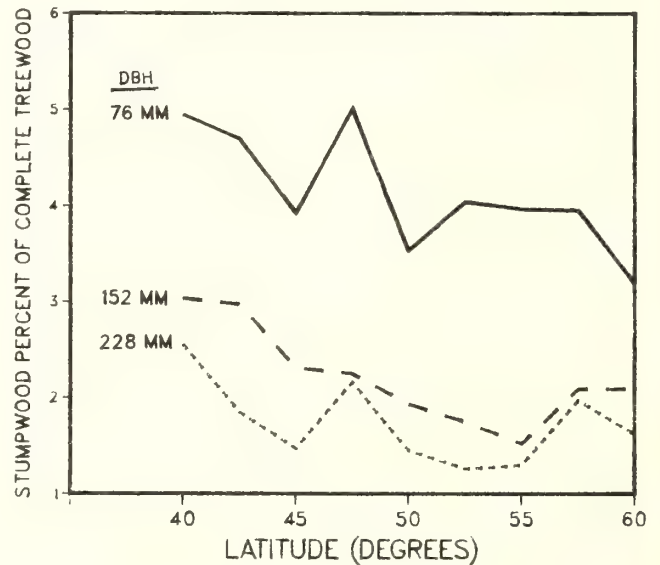


Figure 1-54—Stumpwood as a percentage of complete-tree wood volume related to latitude for *latifolia* trees of three diameters.

1-13 RESULTS—MURRAYANA

For the *murrayana* trees, the three d.b.h. classes averaged 76 mm, with standard deviation of 1.8 mm; 151 mm, with standard deviation of 2.9 mm; and 229 mm, with standard deviation of 3.9 mm. All were selected at medium elevation, which for the four latitudes averaged as follows:

Latitude	Elevation	General location
<i>Degrees</i>	<i>Meters</i>	
37.5	2,402	Just east of Yosemite National Park
40	1,676	Vicinity of Quincy, CA
42.5	2,006	Southwest of Paisley, OR
45	1,148	North of Breitenbush, OR
Average	1,808	

Because the entire *murrayana* sample totaled but 36 trees, correlations among tree characteristics are not noted in the detail provided for the 243 *latifolia* trees. Standard deviations for diameter-class data are noted in parentheses following their average values, as they were in the *latifolia* results section.

Even with this small sample (nine trees per latitude), numerous latitudinal differences were observed. Only those statistically significant are graphed or tabulated. It seems likely from studying the data, however, that had more trees been sampled, statistically significant differences between the two southern latitudes and the two northern latitudes would have been found in many more—perhaps most—of the characteristics measured.

Tree Age

The three diameter classes averaged 67 (25), 84 (34), and 91 (37) years of age measured at 152 mm stump height, but the trees from 42.5 degrees averaged nearly twice the age of those from the other three latitudes (fig. 1-55).

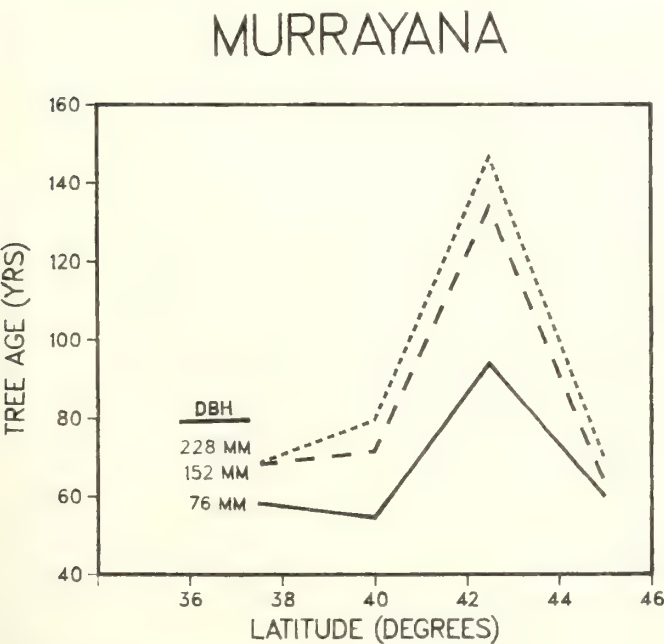


Figure 1-55—Age measured at 152 mm stump height related to latitude for *murrayana* trees of three diameters.

Tree Height to Apical Tip

Tree height was significantly related to d.b.h., but not to latitude; average values were as follows:

Latitude	D.b.h. class		
	76 mm	152 mm	228 mm
	<i>Meters</i>		
<i>Degrees</i>			
37.5	6.1	10.6	15.2
40	6.8	12.3	19.5
42.5	7.8	16.4	20.3
45	8.9	15.6	19.6
Average	7.4	13.7	18.7
	(2.0)	(3.8)	(4.5)

Tree Height to 25-mm Top Diameter (Outside Bark)

Tree height to a 25-mm top diameter was positively correlated with d.b.h., averaging 6.2 (1.9), 12.8 (3.8), and 17.8 (4.5) m for the three diameter classes. Trees were significantly higher at the two northernmost latitudes than at the southern latitudes (fig. 1-56).

Taproot Length

Taproot length, measured from stump top to the end of the portion of the taproot that the field crews were able to extract, was unrelated to latitude but was positively correlated with d.b.h., averaging 58 (14), 91 (13), and 97 (25) cm for the three diameter classes.

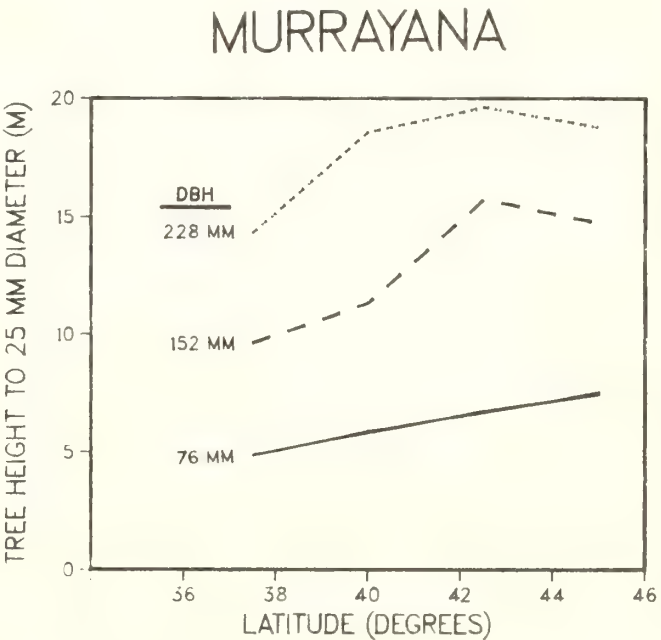


Figure 1-56—Height from stump top to 25-mm stem diameter (measured outside bark) related to latitude for *murrayana* trees of three diameters.

Width of Live Crown

Crown width was positively correlated with d.b.h., averaging 1.30 (0.23), 1.83 (0.23), and 2.64 (0.53) m for the three diameter classes. It differed with latitudinal zone, averaging widest at 37.5 degrees and narrowest at 42.5 degrees (fig. 1-57).

Length of Live Crown

Crown length was unrelated to latitude but was positively correlated with d.b.h., averaging 4.4 (1.6), 7.2 (2.2), and 10.7 (2.3) m for the three diameter classes.

Length of Stem Below Crown

Stem length below crown was positively correlated with d.b.h., averaging 2.98 (1.53), 6.50 (3.67), and 7.99 (3.81) m for the three diameter classes. The southern latitudes averaged shorter in this dimension than the northern latitudes (fig. 1-58).

Stem Crook

Stem crook between 10 and 70 percent of tree height averaged 55 mm, with standard deviation of 37 mm; it was unrelated to either d.b.h. or latitudinal class. We measured the percentage of tree height where maximum crook occurred, but found its location not significantly related to either latitude or diameter class; the average location was at 37 percent of tree height.

Number of Live Branches

The number of live branches per tree was unrelated to latitude, but was positively correlated with d.b.h., averaging 72 (18), 127 (34), and 146 (45) for the three diameter classes.

Average Diameter of Live Branches

Similarly, average diameter of the live branches was unrelated to latitude but was positively correlated with d.b.h., averaging 7.4 (1.6), 11.9 (2.8), and 18.4 (3.6) mm for the three diameter classes.

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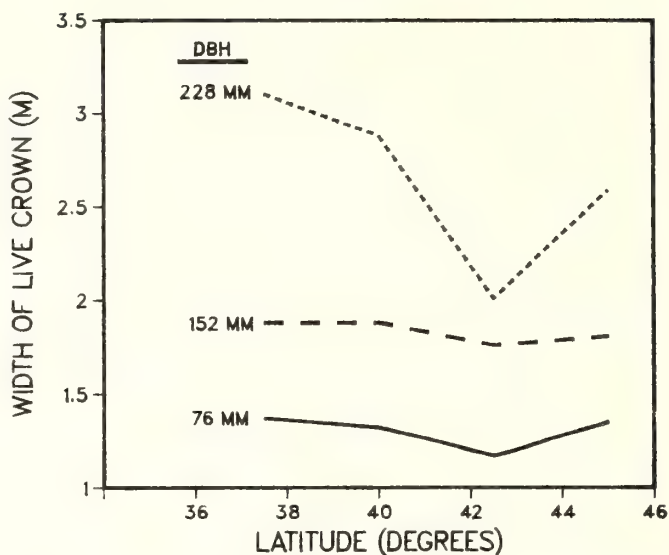


Figure 1-57—Width of live crown of *murrayana* trees of three diameters related to latitude.

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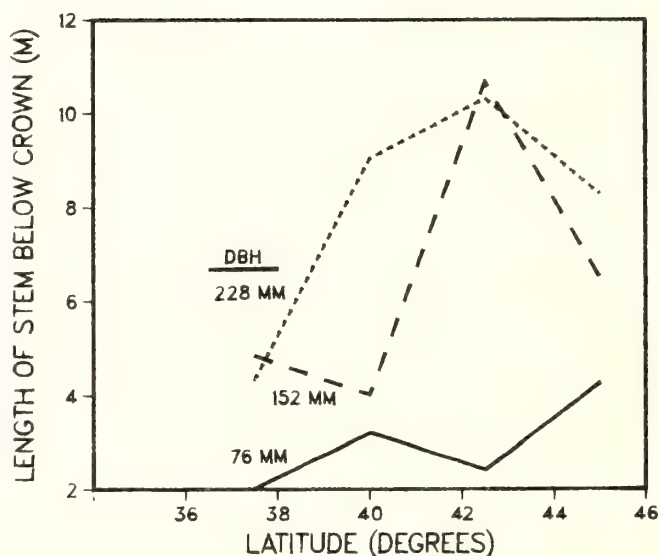


Figure 1-58—Length of stem below live crown of *murrayana* trees of three diameters related to latitude.

Average Live Branch Angle

The average angle between live branches and stem (upward-pointing branches have angles less than 90 degrees; those with drooping branches more than 90 degrees) was greater in small trees than in large, and averaged 88 (9.6), 83 (9.2), and 78 (13.1) degrees for the three diameter classes. Trees in the southern two latitudinal zones averaged 88 degrees, while those in the north averaged 77 degrees (fig. 1-59).

Number of Dead Branches

Number of dead branches was not significantly related to latitude but was positively correlated with d.b.h., averaging 34 (23), 79 (34), and 94 (34) per tree for the three diameter classes.

Stem Diameter (Bark-Free) at Base of Live Crown

Stem diameter at the base of the live crown was not significantly related to latitude but was positively correlated with d.b.h., averaging 58 (12), 108 (17), and 169 (21) mm for the three diameter classes.

Crown Ratio

Crown ratio averaged 0.58, with standard deviation of 0.15. It was unrelated to either diameter class or latitudinal zone.

Average Growth-Ring Width at 152-mm Stump Height

Ring width was positively correlated with d.b.h., averaging 0.7 (0.30), 1.1 (0.42), and 1.6 (0.58) mm for the three diameter classes. Growth rings were significantly narrower in trees from 42.5 degrees latitude (fig. 1-60).

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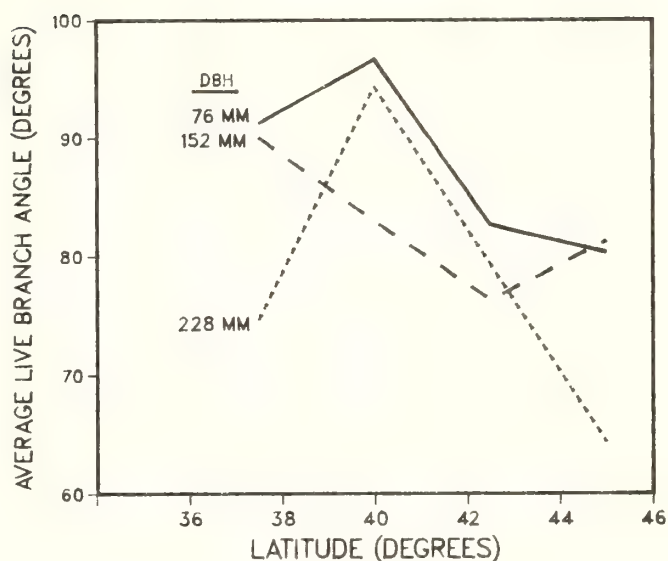


Figure 1-59—Average live branch angle, measured between stem surface above branch and branch top surface adjacent to its entry into stem, related to latitude for *murrayana* trees of three diameters.

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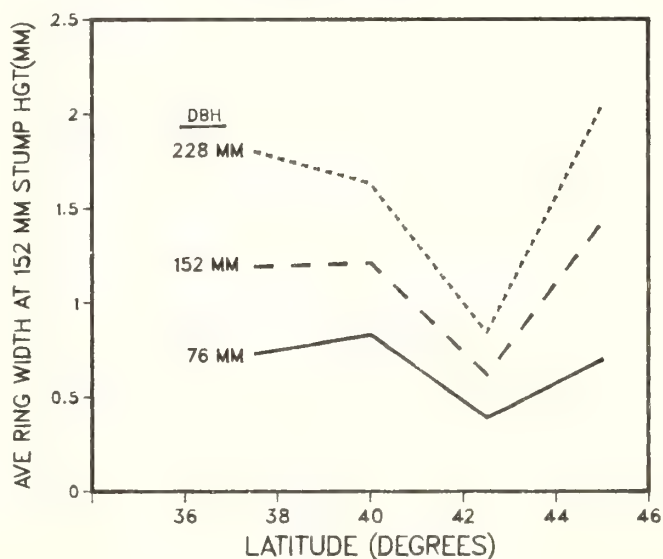


Figure 1-60—Average growth ring width at 152 mm stump height related to latitude for *murrayana* trees of three diameters.

Number of Cones on Tip 305 mm of the Top 25 Branches

Of the 12 trees in each d.b.h. class, 10 of the 76-mm trees, two of the 152-mm trees, and two of the 228-mm trees had no cones on the tip 305 mm of the top 25 branches. The aggregate number of cones on this portion of the top 25 branches was positively correlated with d.b.h., averaging 1.3 (3.7), 7.4 (8.9), and 18.4 (19.7) cones per tree for the three diameter classes. Trees from latitude 42.5 degrees had most cones on these branch sections and trees from 40 degrees least, as follows:

Latitude Degrees	D.b.h. class		
	76 mm	152 mm	228 mm
	----- Number of cones -----		
37.5	0	7.0	12.3
40	0	1.7	4.0
42.5	0	16.3	40.7
45	5	4.7	16.7

Total Number of Cones per Tree (Calculated)

The calculated total number of cones per tree was unrelated to latitude but was positively correlated with d.b.h., averaging 10 (25), 48 (42), and 165 (100) for the three diameter classes.

Cone Serotiny

All of the trees bearing cones were classified as open-coned; that is, more than 80 percent of the cones were open on each tree that had cones.

Branchbark Thickness (Measured With a Scale)

Branchbark thickness was unrelated to latitude but was positively correlated with d.b.h., averaging 1.1 (0.20), 1.2 (0.25), and 1.3 (0.33) mm for the three diameter classes.

Central Rootbark Thickness (Measured With a Scale)

Central rootbark thickness was unrelated to latitude but was positively correlated with d.b.h., averaging 2.8 (0.74), 3.8 (1.11), and 5.4 (1.82) mm for the three diameter classes.

Lateral Rootbark Thickness (Measured With a Scale)

Bark thickness of the lateral roots was positively correlated with d.b.h., averaging 2.2 (0.45), 2.8 (0.75), and 3.4 (0.94) mm for the three diameter classes. Thickest bark (3.4 mm average for nine trees) was observed in the southernmost latitude, while the three more northerly latitudes averaged 2.6 mm (fig. 1-61).

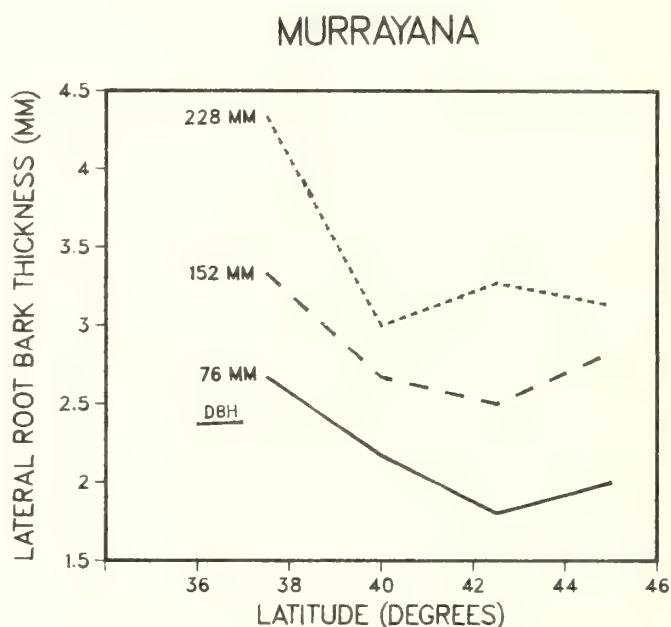


Figure 1-61—Lateral rootbark thickness related to latitude for *murrayana* trees of three diameters.

Stumpbark Thickness (Measured With a Scale)

Bark thickness of the stump between groundline and 152-mm stump height was unrelated to latitude but was positively correlated with d.b.h., averaging 3.6 (0.85), 5.4 (1.70), and 7.2 (1.25) mm for the three diameter classes.

Stembark Thickness (Measured With a Diameter Tape)

Stembark thickness was positively correlated with d.b.h., averaging 2.3, 3.7, and 4.7 mm for the three diameter classes (data for all 10 heights in each tree pooled); it was maximum at stump height and diminished in ogee-curve form with height in tree (fig. 1-62).

Trees in latitudinal zones 37.5 and 40 degrees had thicker bark than those in zones of 42.5 and 45 degrees (fig. 1-63).

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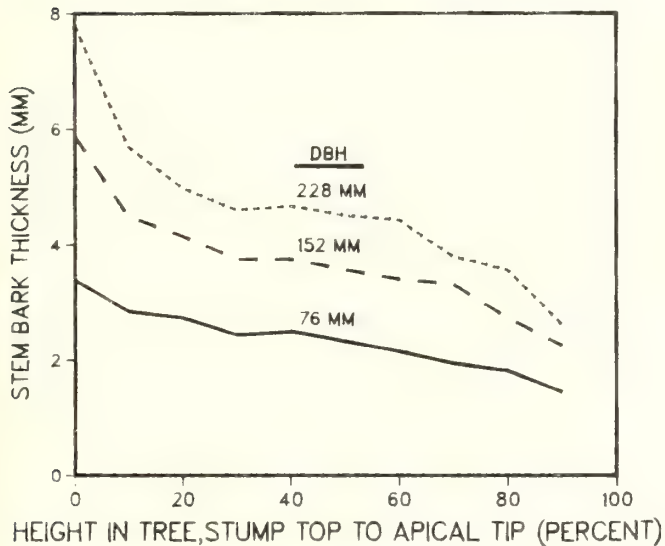


Figure 1-62—Stembark thickness related to height in tree for *murrayana* trees of three diameters; latitudinal data pooled.

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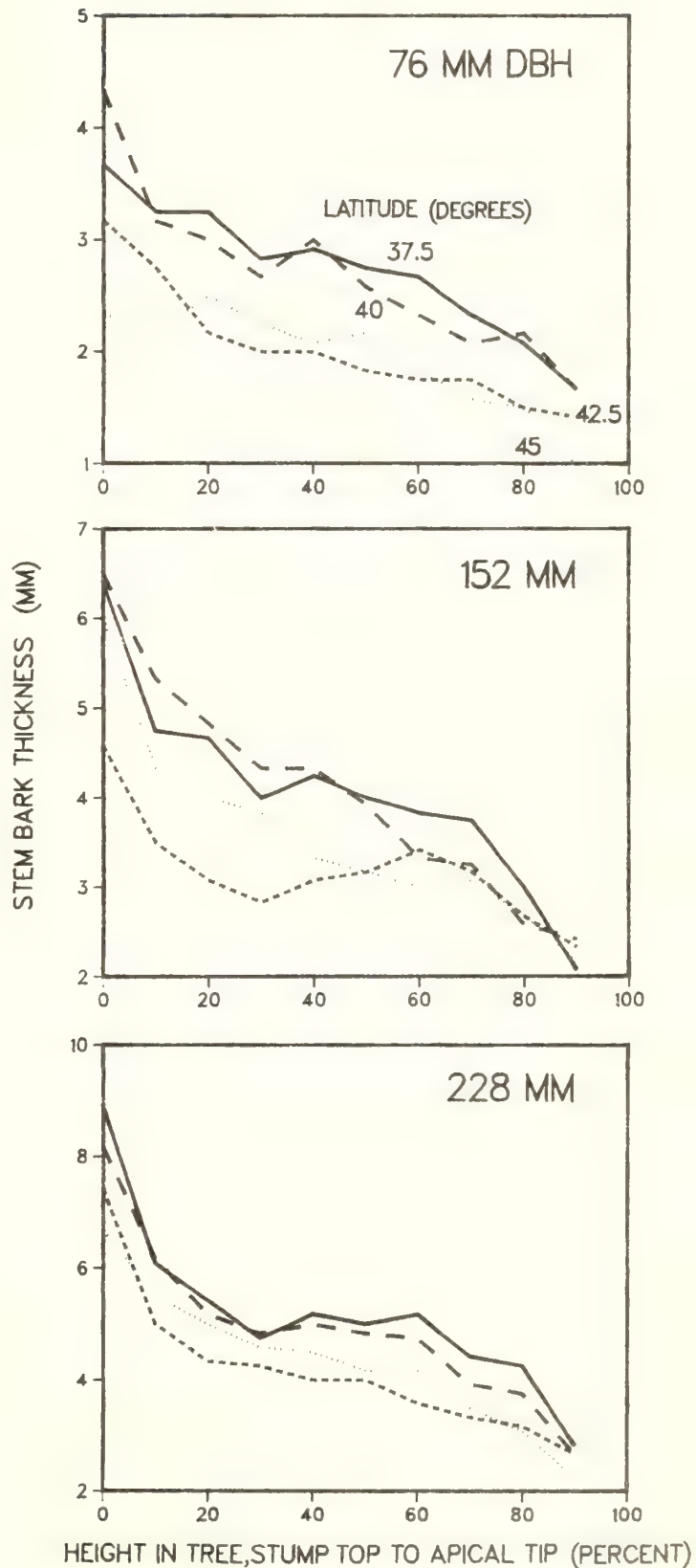


Figure 1-63—Stembark thickness related to latitude and height in stem for *murrayana* trees of three diameters.

Total Volume of Dead Branches (Thousand cm³)

Volume of dead branches on each tree was positively correlated with d.b.h., averaging 0.4 (0.30), 1.7 (1.10), and 8.8 (2.46) for the three diameter classes. Trees 76 mm in d.b.h. had dead-branch volume positively correlated with latitude (fig. 1-64). In the 40-degree zone trees of all diameters averaged twice the dead-branch volume of those in more southerly zones.

Volume of Live Branches, Wood Plus Bark (Thousand cm³)

Total volume was unrelated to latitude but was positively correlated with d.b.h., averaging 1.4 (0.59), 8.9 (3.24), and 30.9 (14.46) for the three diameter classes.

Volume of Live Branchwood (Thousand cm³)

Similarly, live branchwood volume was unrelated to latitude but was positively correlated with d.b.h., averaging 0.7 (0.30), 5.1 (1.76), and 19.6 (7.80) for the three diameter classes.

Volume of Live Branchbark (Thousand cm³)

Live branchbark volume also was unrelated to latitude but was positively correlated with d.b.h., averaging 0.7 (0.30), 3.8 (1.60), and 11.3 (6.97) for the three diameter classes.

Volume of Stump-Root System, Wood Plus Bark (Thousand cm³)

Stump-root system volume, including both wood and bark, was unrelated to latitude but was positively correlated with d.b.h., averaging 3.9 (1.09), 21.0 (5.31), and 45.7 (6.52) for the three diameter classes.

Volume of Stump, Wood Plus Bark (Thousand cm³)

Total stump volume (groundline to 152 mm stump top) was unrelated to latitude but was positively correlated with d.b.h., averaging 1.2 (0.36), 4.6 (1.55), and 7.1 (1.71) for the three diameter classes.

Volume of Lateral Roots, Wood Plus Bark (Thousand cm³)

Lateral root volume (root collar to a radius 305 mm from stump pith) was positively correlated with tree d.b.h., averaging 0.7 (0.29), 6.5 (2.55), and 16.1 (0.94) for the three diameter classes. Trees 152 and 228 mm in d.b.h. had maximum lateral root volume at 40 degrees of latitude; volumes were lowest or nearly so at 45 degrees (fig. 1-65).

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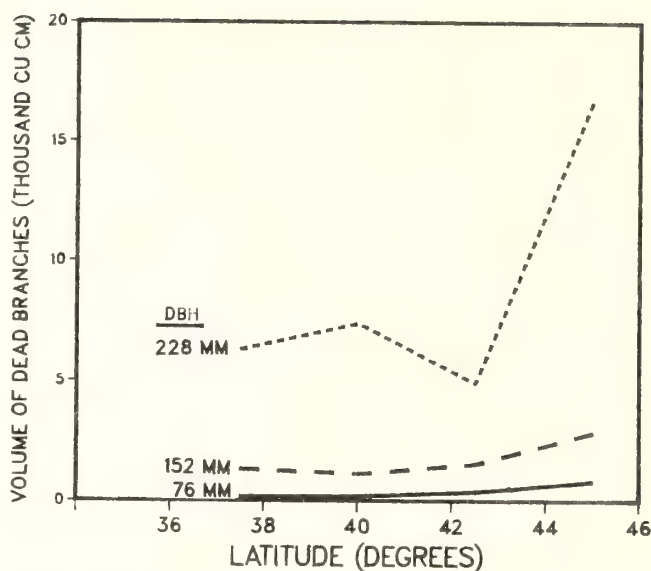


Figure 1-64—Dead-branch volume related to latitude for *murrayana* trees of three diameters.

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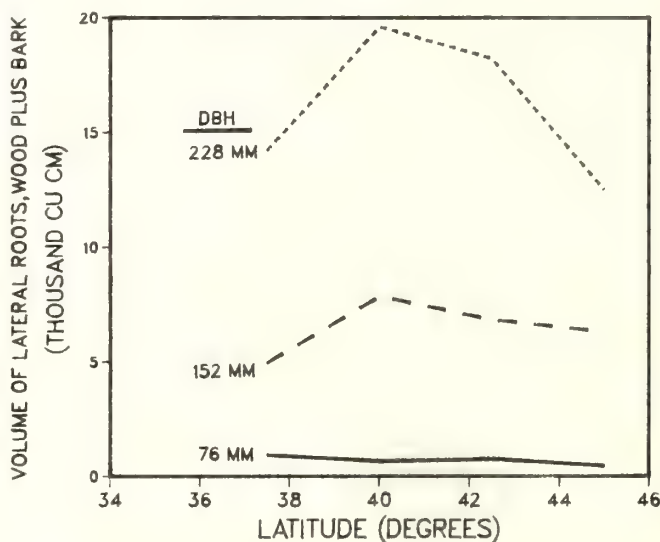


Figure 1-65—Lateral root volume, wood plus bark, related to latitude for *murrayana* trees of three diameters.

Volume of Central Root Mass, Wood Plus Bark (Thousand cm³)

The central root mass shorn of laterals and stump, but with that portion of the taproot recovered by the field crews, had volume unrelated to latitude, but positively correlated with tree d.b.h., averaging 2.0 (0.71), 10.0 (2.61), and 22.4 (5.00) for the three diameter classes.

Volume of Stump-Root System, Wood Only (Thousand cm³)

The stump-root system wood volume was positively correlated with d.b.h., averaging 3.2 (0.91), 17.0 (6.42), and 41.3 (5.71) for the three diameter classes. Wood volume was greatest at 40 degrees and least in the 45-degree latitudinal zone (fig. 1-66).

Volume of Stump, Wood Only (Thousand cm³)

Stumpwood volume was unrelated to latitude but was positively correlated with d.b.h., averaging 1.1 (0.30), 4.5 (1.58), and 6.4 (1.54) for the three diameter classes.

Volume of Lateral Roots, Wood Only (Thousand cm³)

Wood volume of lateral roots was unrelated to latitude but was positively correlated with d.b.h., averaging 0.5 (0.23), 5.6 (2.37), and 14.1 (3.45) for the three diameter classes.

Volume of Central Root Mass, Wood Only (Thousand cm³)

Wood volume of the central root mass shorn of stump and laterals, but including taproot, was unrelated to latitude but was positively correlated with d.b.h., averaging 1.5 (0.69), 8.3 (2.96), and 20.7 (4.54) for the three diameter classes.

Volume of Stump-Root System, Bark Only (Thousand cm³)

Bark volume of the stump-root system was unrelated to latitude but was positively correlated with d.b.h., averaging 0.6 (0.19), 2.6 (0.91), and 4.4 (1.11) for the three diameter classes.

Volume of Stump, Bark Only (Thousand cm³)

Bark volume from stump top to ground level was positively correlated with d.b.h., averaging 0.18 (0.06), 0.51 (0.17), and 0.67 (0.22) for the three diameter classes. Stumpbark volume was usually least at 45 degrees and greatest in the southern latitudes (fig. 1-67).

Volume of Lateral Roots, Bark Only (Thousand cm³)

Bark volume of lateral roots from root collar to a radius of 305 mm from stump pith was unrelated to latitude but was positively correlated with d.b.h., averaging 0.2 (0.07), 1.0 (0.58), and 2.0 (0.76) for the three diameter classes.

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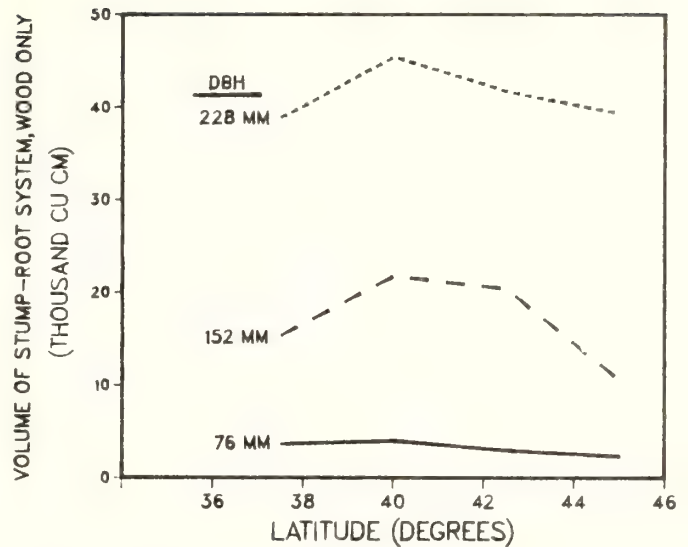


Figure 1-66—Wood volume in stump-root system of *murrayana* trees of three diameters related to latitude.

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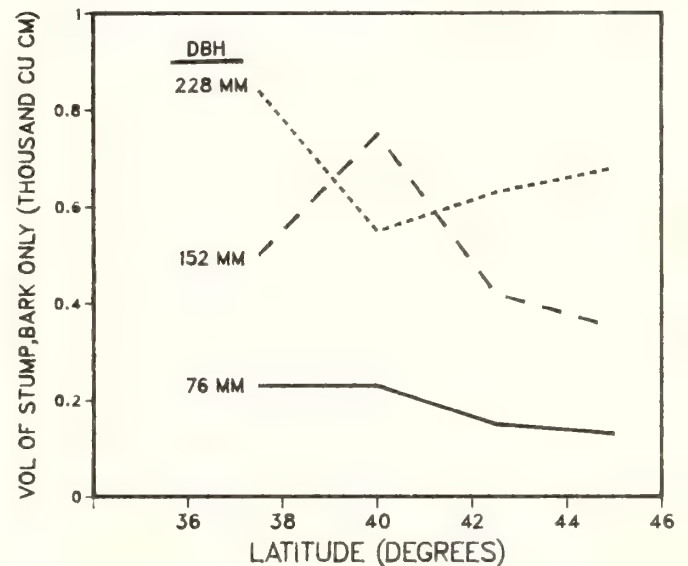


Figure 1-67—Bark volume in stump of *murrayana* trees of three diameters related to latitude.

Volume of Central Root Mass, Bark Only (Thousand cm³)

Volume of bark on the central root mass, including taproot, was unrelated to latitude but was positively correlated with d.b.h., averaging 0.3 (0.11), 1.0 (0.37), and 1.7 (0.56) for the three diameter classes.

Stem Volume to Apical Tip, Wood Plus Bark (Thousand cm^3)

Total stem volume was unrelated to latitude but was positively correlated with d.b.h., averaging 18.5 (4.5), 124.2 (39.4), and 367.4 (105.0) for the three diameter classes.

Stemwood Volume to Apical Tip (Thousand cm^3)

Similarly, stemwood volume to the apical tip was unrelated to latitude but was positively correlated with d.b.h., averaging 15.8 (4.1), 111.1 (6.6), and 336.1 (98.5) for the three diameter classes.

Stembark Volume to Apical Tip (Thousand cm^3)

Stembark volume to the apical tip was unrelated to latitude; for the three diameter classes it averaged 2.7 (0.50), 13.2 (3.24), and 31.3 (6.79).

Complete-Tree Volume, Wood Plus Bark (Thousand cm^3)

Complete-tree volume of wood plus bark (stump-root system, stem, live and dead branches—but not foliage) was unrelated to latitude but positively correlated with d.b.h., averaging 24.2 (4.72), 156.0 (38.7), and 452.7 (97.14) for the three diameter classes.

Complete-Tree Volume, Wood Only (Thousand cm^3)

Complete-tree volume of wood was unrelated to latitude but was positively correlated with d.b.h., averaging 20.2 (0.3), 136.4 (36.8), and 405.8 (95.5).

Complete-Tree Volume, Bark Only (Thousand cm^3)

Bark volume of complete trees was unrelated to latitude but was positively correlated with d.b.h., averaging 4.1 (0.73), 19.6 (2.83), and 46.9 (6.71) for the three diameter classes.

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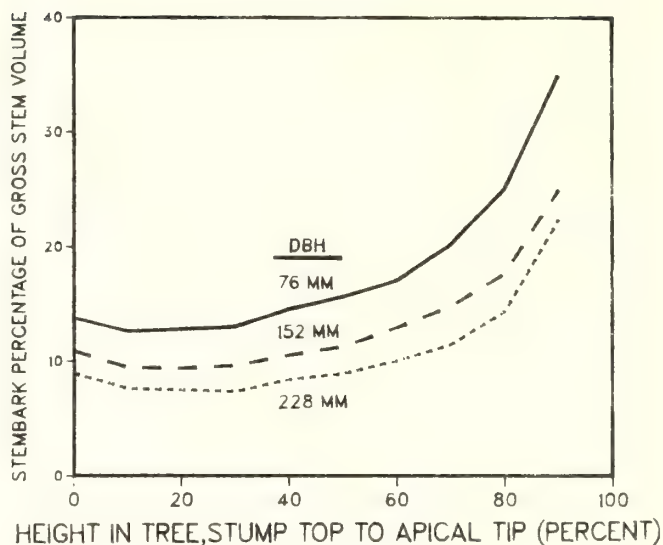


Figure 1-68—Stembark percentage of gross stem volume at 10 heights in *murrayana* trees of three diameters; latitudinal data pooled.

Stembark as Percentage of Gross Stem Volume by Height in Tree

In all diameter classes, bark percentage was relatively large at stump height, decreased from stump height to 20 percent of tree height, and then was positively correlated with height in tree (fig. 1-68); large-diameter trees had less percentage of stembark volume at all stem heights than small-diameter trees.

Trees in latitudinal zones 37.5 and 40 degrees had a greater percentage of stembark at all heights than those from latitudes 42.5 and 45 degrees; the 42.5-degree zone had trees with least percentage of stembark volume (fig. 1-69).

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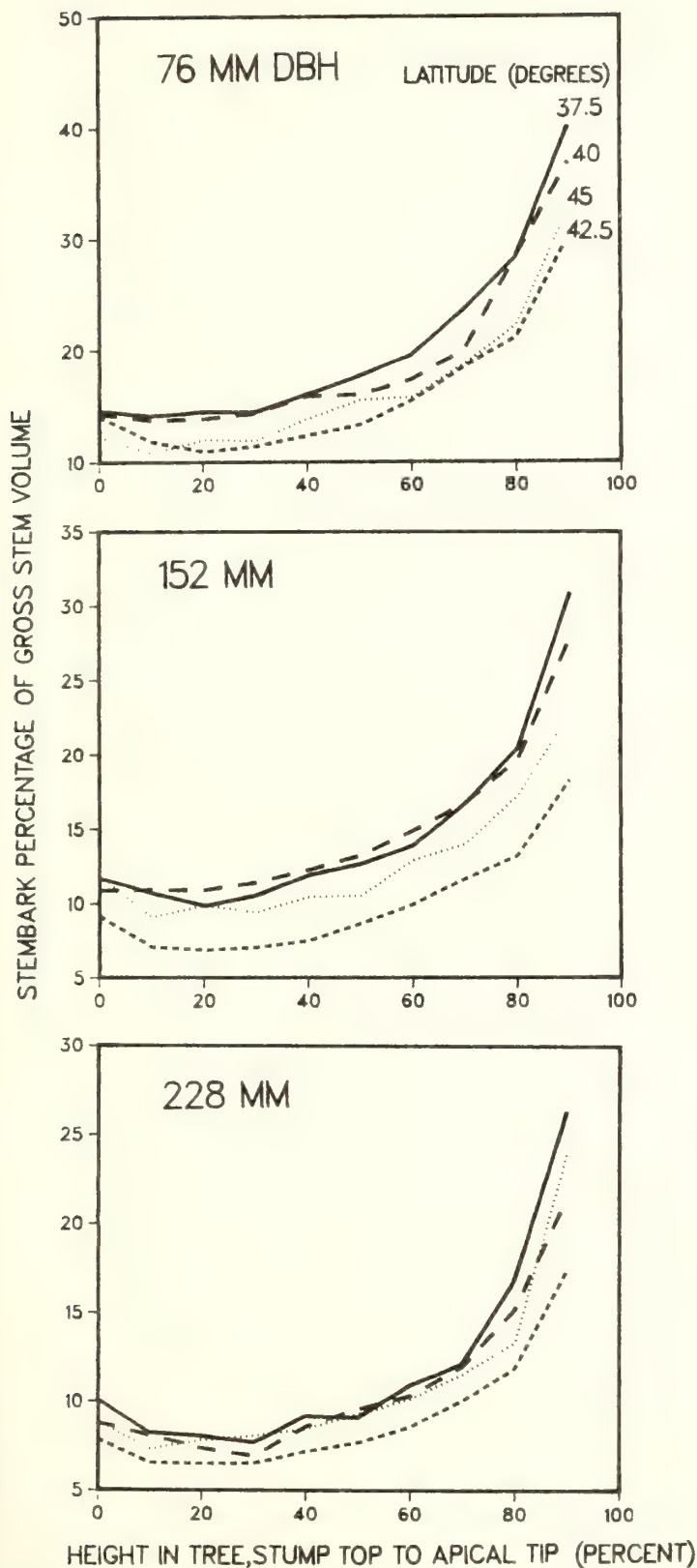


Figure 1-69—Stembark percentage of gross stem volume related to latitude and height in tree for *murrayana* trees of three diameters.

Stembark as Percentage of Gross Stem Volume

Stembark volume as a percentage of gross volume of stem from stump top to apical tip was negatively correlated with d.b.h., averaging 14.8 (2.0), 11.0 (1.7), and 8.7 (1.0) percent for the three diameter classes; that is, small trees had a greater percentage of stembark than large trees.

Trees in the southernmost latitudinal zone had the greatest percentage of stembark volume, averaging 12.6 percent; those at 42.5 degrees least, averaging 10.0 percent (fig. 1-70).

Stump-Root Bark as Percentage of Gross Stump-Root System Volume

Stump-root bark volume as a percentage of gross volume of stump-root system was unrelated to latitude, but, as in stems, was inversely correlated with d.b.h., averaging 16.7 (1.6), 12.3 (2.0), and 9.5 (1.6) percent for 76-, 152-, and 228-mm trees, respectively.

Live Branchbark as Percentage of Gross Live Branch Volume

Percentage of branchbark in gross live branch volume was unrelated to latitude but was inversely correlated with tree d.b.h., averaging 52.3 (4.4), 42.0 (4.9), and 34.7 (7.0) percent for 76-, 152-, and 228-mm trees, respectively.

MURRAYANA

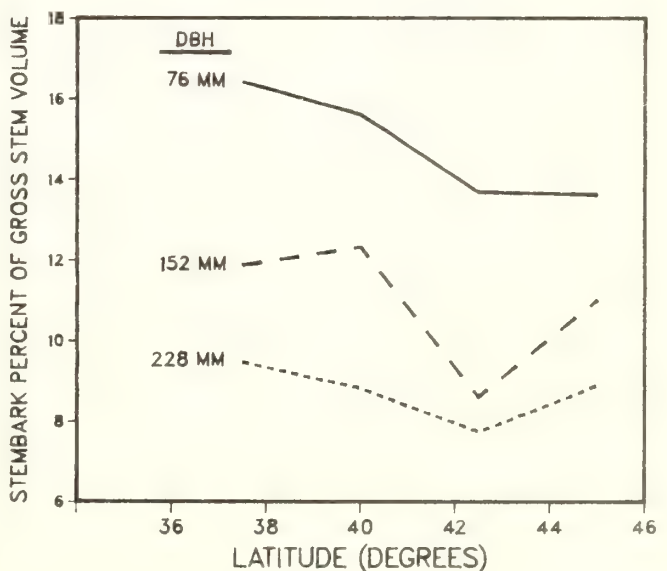


Figure 1-70—Stembark percentage of gross stem volume (stump top to apical tip) related to latitude for *murrayana* trees of three diameters.

Bark of Complete Tree as Percentage of Complete-Tree Volume

Complete-tree bark as a percentage of complete-tree volume was inversely correlated with d.b.h., averaging 17.1 (2.8), 13.0 (2.5), and 10.8 (3.0) percent for 76-, 152-, and 228-mm trees.

In the southernmost latitudinal zone (37.5 degrees) percentage of complete-tree bark was highest (15.9 percent with diameter data pooled); it was lowest at 42.5 degrees, where it averaged only 11.4 percent (fig. 1-71).

Stemwood as Percentage of Complete-Tree Wood Volume

Stemwood volume averaged 79.8 (6.66) percent of complete-tree volume and was unrelated to tree diameter. It was least in the southern latitudes and most in the northern latitudes, averaging 75.1, 77.6, 83.9, and 82.6 percent for latitudes 37.5, 40, 42.5, and 45 degrees, respectively.

Live Branchwood as Percentage of Complete-Tree Wood Volume

Live branchwood as a percentage of complete-tree wood volume was unrelated to latitude but was positively correlated with d.b.h., averaging 3.6 (1.90), 4.3 (2.58), and 5.5 (3.81) for 76-, 152-, and 228-mm trees.

MURRAYANA

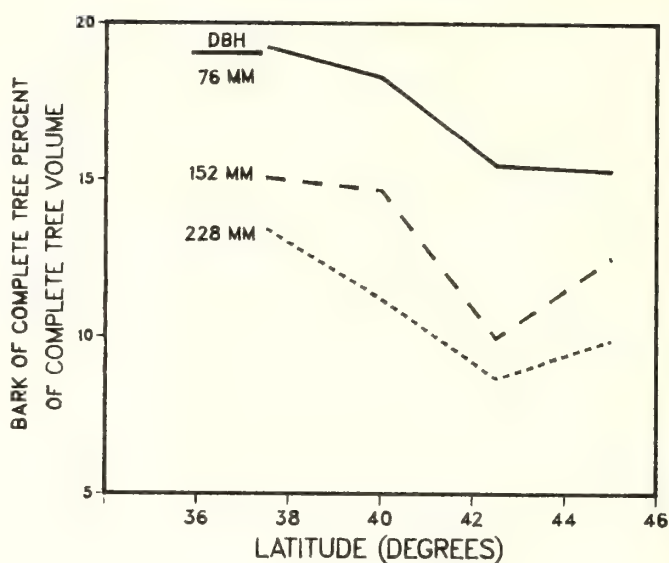


Figure 1-71—Bark volume of complete tree as a percentage of volume of complete tree, wood plus bark, related to latitude for *murrayana* trees of three diameters.

Dead Branchwood as Percentage of Complete-Tree Wood Volume

Dead branchwood volume averaged 1.9 (1.49) percent of complete-tree volume and was unrelated to tree diameter. Percentage of dead branchwood was greatest in the most northerly latitudinal zone where it averaged 3.4 percent; for 76-mm trees only, it was positively correlated with latitude, as follows:

Latitude Degrees	D.b.h. class		
	76 mm	152 mm	228 mm
37.5	0.92	1.40	1.80
40	1.05	1.09	1.81
42.5	2.03	.91	1.06
45	4.01	1.97	4.19
Average	2.00 (1.49)	1.34 (.83)	2.22 (1.92)

Stumpwood as Percentage of Complete-Tree Wood Volume

From groundline to 152-mm-high stump top, stumpwood as a percentage of complete-tree wood varied inversely with d.b.h., averaging 5.4 (1.74), 3.6 (1.68), and 1.7 (0.56) percent for 76-, 152-, and 228-mm trees. With diameters pooled, this percentage averaged greatest (4.5 percent) at 40 degrees latitude and least (2.7 percent) at 45 degrees (fig. 1-72).

Stump-Root System Wood as Percentage of Complete-Tree Wood Volume

Total stump-root system wood (stump, central root collar and taproot, and laterals to 305 mm radius from stump pith) as a percentage of complete-tree wood volume was inversely correlated with d.b.h., averaging 16.5 (5.2), 13.3 (6.2), and 10.7 (2.7) percent for 76-, 152-, and 228-mm trees. Stump-root wood volume percentage averages were smallest (9.0) in the northernmost latitudinal zone and highest (16.5) in the two southernmost zones (fig. 1-73).

MURRAYANA

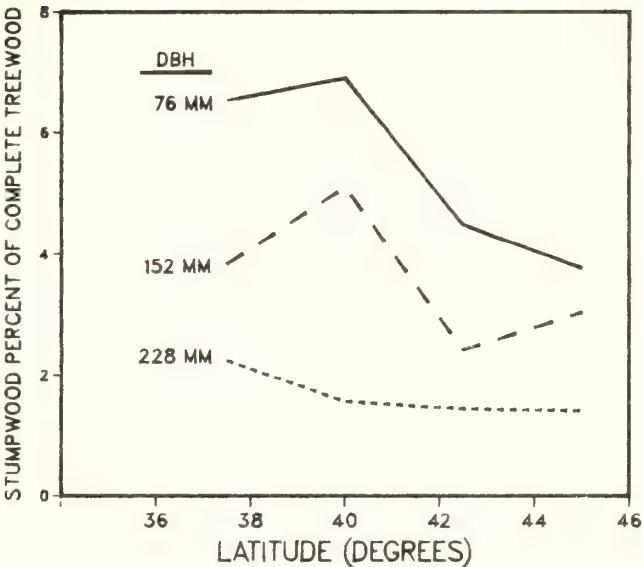


Figure 1-72—Stumpwood percentage of complete-tree wood volume related to latitude for *murrayana* trees of three diameters.

MURRAYANA

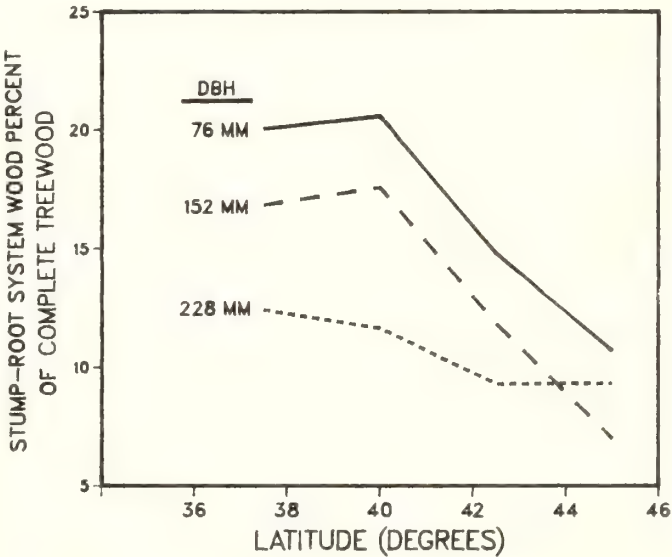


Figure 1-73—Wood volume of the stump-root system as a percentage of complete-tree wood volume related to latitude for *murrayana* trees of three diameters.

1-14 RESULTS—*LATIFOLIA* COMPARED TO *MURRAYANA*

The experimental design permitted an orthogonal comparison between the two varieties at three latitudes, as follows:

Varieties:	(2)	<i>latifolia</i> and <i>murrayana</i>
D.b.h. classes:	(3)	76, 152, and 228 mm
Latitudinal zones:	(3)	40, 42.5, and 45 degrees
Elevational zones:	(1)	medium
Replications:	(3)	

Sample size for this comparison therefore totaled 54 trees, 27 of each variety. Sample locations and average elevations were as follows:

Variety and latitude	Elevation	General location
Degrees	Meters	
<i>murrayana</i>		
40	1,676	Vicinity of Quincy, CA
42.5	2,006	Southwest of Paisley, OR
45	1,148	North of Breitenbush, OR
<i>latifolia</i>		
40	2,711	Between Boulder, CO, and Meeker, UT
42.5	2,376	Between Lander, WY, and Soda Springs, UT
45	1,930	Between the Gallatin River, MT, and north of John Day, OR

In the discussions that follow, only significant relationships associated with varietal differences are explained; the other effects are more completely described in the previous two results sections.

Tree Age

At 42.5 degrees, *murrayana* trees (diameters pooled) averaged 125 years old vs. only 89 for *latifolia*; but at 40 and 45 degrees, *murrayana* trees averaged younger than *latifolia*—67 vs. 88 years.

Average Diameter of Live Branches (50 mm from Stem)

Live branch diameter was about 2 mm less on *murrayana* trees than on *latifolia*.

Average Live Branch Angle

In latitudinal zones 40 and 42.5 degrees, live branch angle averaged greater on *murrayana* than on *latifolia* trees—85 vs. 75 degrees; at 45 degrees of latitude differences varied with tree d.b.h. (fig. 1-74).

COMPARISON

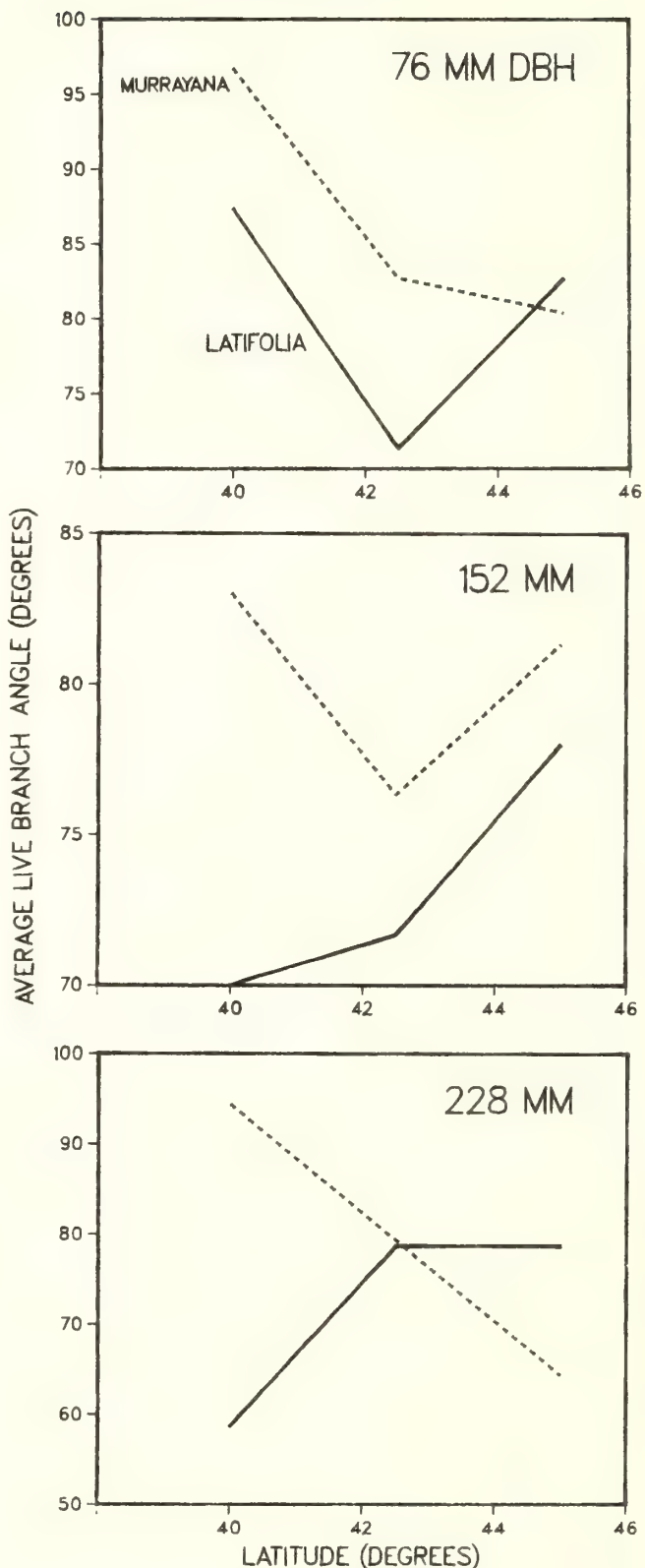


Figure 1-74—Average live branch angles of *murrayana* trees of three diameters compared with those of *latifolia* related to latitude.

Average Growth-Ring Width at 152-mm Stump Height

At 42.5 degrees latitude, *murrayana* had average ring width of only 0.6 mm, whereas *latifolia* ring width averaged 1.0 mm. At the other two latitudes, however, *murrayana* rings averaged wider than those of *latifolia*—1.3 mm vs. 0.9 mm.

Number of Cones on Tip 305 mm of the Top 25 Branches

Latifolia trees had almost four times more cones on the tip 305 mm of the top 25 branches than *murrayana*, as follows:

Latitude	<i>Latifolia</i>	<i>Murrayana</i>
Degrees	- - - - - Number - - - - -	
40	25	2
42.5	70	19
45	16	9
Average	37	10

Total Number of Cones per Tree (Calculated)

With diameters and latitudes pooled, calculated total number of cones per *latifolia* tree was more than three times that per *murrayana* tree—279 vs. 80.

Cone Serotiny

Murrayana trees were all classified as open-coned trees, whereas the degree of serotiny of *latifolia* trees depended on latitudinal zone. *Latifolia* trees in northern latitudes were mostly classified as closed-coned; those in the southern latitudes were mostly open-coned (fig. 1-19).

Central Rootbark Thickness (Measured With a Scale)

At latitudes 42.5 and 45 degrees, central rootbark was thicker on *latifolia* than on *murrayana* trees—averaging 4.3 mm vs. 3.6 mm; at 40 degrees, however, *murrayana* bark was the thickest—4.3 mm vs. 3.5 mm for *latifolia*.

Lateral Rootbark Thickness (Measured With a Scale)

On lateral roots, *latifolia* bark was thicker than that of *murrayana* at all latitudes, averaging for all diameters and latitudes 3.1 mm vs. 2.6 mm.

Stumpbark Thickness (Measured With a Scale)

Similarly, average thickness of stumpbark was greater for *latifolia* than for *murrayana*—5.8 mm vs. 5.1 mm, with all diameters and latitudes pooled.

Stembark Thickness (Measured With a Diameter Tape)

From stump top through 40 percent of tree height, *murrayana* stembark (diameter and latitudinal data pooled) was slightly thicker than that of *latifolia*—4.1 mm vs. 4.0 mm. At 50 percent of tree height both varieties had equal bark thickness—3.3 mm. From 60 to 90 percent of tree height, *latifolia* had slightly thicker stembark than *murrayana*—2.9 mm vs. 2.7 mm.

Volume of Stump, Wood Plus Bark (Thousand cm³)

In 152-mm trees at 40 degrees, the average stump volume of wood plus bark was greater in *murrayana* (6.7) than in *latifolia* (4.7). The overall averages for all diameters and latitudes indicated that stumps of *murrayana* had less gross volume (4.3) than *latifolia* (4.8), however.

Volume of Central Root Mass, Wood Plus Bark (Thousand cm³)

The gross central root volume was not greatly different for the two varieties except at 40 degrees latitude, where 152- and 228-mm *latifolia* trees had much greater volume (23 and 73) than *murrayana* (11 and 24).

Volume of Stump, Wood Only (Thousand cm³)

In 76-mm trees the two varieties had equal volumes of wood in the stump (1.0). The 152-mm *murrayana* trees averaged more stumpwood volume than *latifolia* (4.8 vs. 4.1); in 228-mm trees, however, the *murrayana* trees had less stumpwood volume (6.3 vs. 7.8).

Volume of Central Root Mass, Wood Only (Thousand cm³)

Wood volume in the central root mass was not greatly different in the two varieties, except that 76-mm *murrayana* trees at 40 degrees had much greater wood volume than *latifolia* (2.3 vs. 1.2).

Volume of Stump, Bark Only
(Thousand cm³)

Except for 76- and 152-mm trees at 40 degrees latitude, bark volume in the stump from groundline to 152-mm-high stump top was greater in *latifolia* than in *murrayana* trees (fig. 1-75).

Stembark as Percentage of Gross Stem
Volume by Height in Tree

At latitude 40 degrees, *murrayana* had—at each height sampled—about 2 percentage points more bark volume as a percentage of gross stem volume than *latifolia*.
At latitude 42.5 degrees, however, *latifolia* had—at each height sampled—about 1 percentage point more bark volume as a percentage of gross stem volume than *murrayana*.

At latitude 45 degrees, bark volume percentages at all heights sampled were about equal for the two varieties.
The overall latitudinal comparison is shown by the following tabulation for stembark percentage of entire gross stem volume (diameter data pooled):

Latitude Degrees	Latifolia ----- Percent -----	Murrayana
40	10.9	12.3
42.5	11.0	10.0
45	11.3	11.2

Live Branchbark as Percentage of Gross
Live Branch Volume

With diameter data pooled, *murrayana* averaged more live branchbark as a percentage of live branch gross volume than *latifolia*, as follows:

Latitude Degrees	Latifolia ----- Percent -----	Murrayana
40	34.5	46.5
42.5	38.1	39.2
45	41.5	42.2
Average	38.0	42.6

Stump-Root System Wood as Percentage
of Complete-Tree Wood Volume

With diameter data pooled, *murrayana* averaged more stump-root system wood as a percentage of complete-tree wood volume than *latifolia* in the two southern latitudinal zones, as follows:

Latitude Degrees	Latifolia ----- Percent -----	Murrayana
40	11.3	12.5
42.5	10.8	12.0
45	11.1	9.0
Average	11.1	12.5

COMPARISON

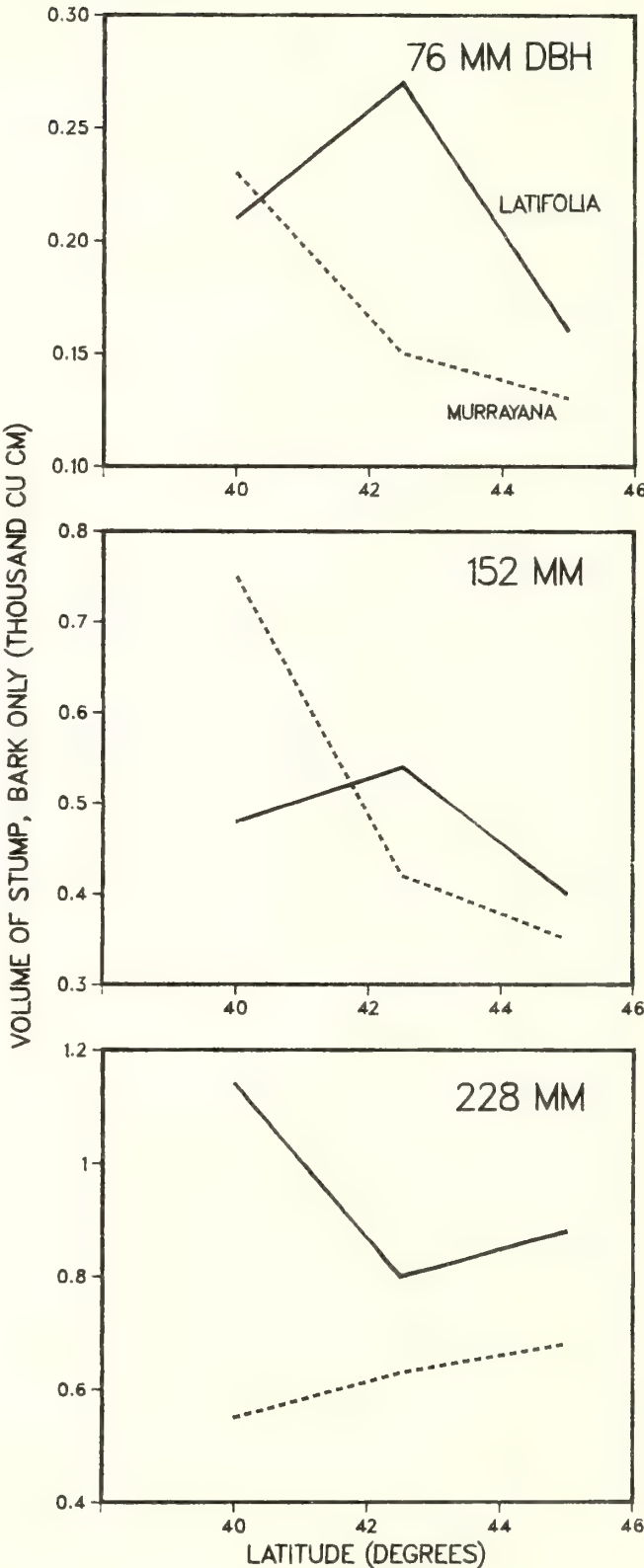


Figure 1-75—Volume of bark in stumps of *murrayana* trees of three diameters compared with volume in *latifolia* related to latitude.

1-15 SUMMARY OF RESULTS

Latifolia

Throughout the latitudinal range sampled (40 through 60 degrees), trees 76-, 152-, and 228-mm d.b.h. averaged 71, 91, and 107 years of age, respectively; trees of equal diameter were older if taken from high elevation than low. The medium-elevation zone for *latifolia* decreased from about 2,700 m at latitude 40 degrees to about 750 m at 60 degrees.

The three diameter classes averaged 9.3, 15.6, and 19.1 m in height; trees were tallest at latitudes 50 through 55 degrees, and—except in the middiameter class—were tallest at low elevation and shortest at high elevation.

Of all the tree characteristics measured, root system dimensions and volumes were most closely correlated with other major tree characteristics. Taproot length was positively correlated with d.b.h., averaging 554, 778, and 942 mm for the three diameter classes.

Crown width was more closely correlated with other tree characteristics than crown length. Crown ratio was unrelated to d.b.h., and averaged 0.46 for the 243 trees sampled.

Stem length below crown was positively correlated with d.b.h., and averaged 5.0, 8.8, and 10.9 m for the three diameter classes; latitudes 50 through 55 degrees had trees with the longest stem length below crown.

Stem crook (sweep) between 10 and 70 percent of tree height averaged 43 mm and was unrelated to d.b.h. or elevational zone; midlatitude trees had less stem crook than those in the south or the north of the range.

The number of live branches per tree averaged 64, 108, and 133 for trees 76-, 152-, and 228-mm d.b.h.; mean branch diameter for these trees was 9, 13, and 19 mm, respectively, with branch angles averaging 85, 79, and 77 degrees.

The number of dead branches per tree was unrelated to elevational zone, and averaged 57, 100, and 119 for the three diameter classes; fewest were observed in latitudes 42.5 through 47.5 degrees, most in latitudes 50 through 57.5 degrees.

Stem diameter at the base of the live crown was proportional to d.b.h., averaging 52, 100, and 148 mm for the three diameter classes.

Growth-ring width measured at 152-mm stump height was positively correlated with d.b.h., averaging 0.67, 1.01, and 1.33 mm for the three diameter classes.

Only 191 of the 243 trees had cones on the tip 305 mm of the top 25 branches; their number—and the total number of cones on each tree—was positively correlated with d.b.h. Southern latitudes had more open-coned trees than those in northern latitudes; at 52.5 degrees and farther north virtually all of the trees were classified as closed-coned (fig. 1-19).

Complete-tree volume of wood plus bark (stump-root system, stem, live and dead branches—but not foliage) averaged 31.0, 191.1, and 509.0 thousand cm³ for the three diameter classes. Trees at high elevation had least volume. Complete-tree volumes averaged minimum at 40 degrees; they averaged maximum in latitudinal zones 50 through 55 degrees.

The proportion of complete-tree wood volumes comprised of wood from each of the tree portions averaged as follows:

Tree portion	Tree d.b.h., mm		
	76	152	228
	- - - Percent - - -		
Stem to apical tip	81	83	82
Live branches	3	4	6
Dead branches	2	2	2
Stump-root system to 305 mm radius from stump pith	14	11	10
Total	100	100	100

The bark percentage of gross (wood-plus-bark) volume of each tree component averaged as follows:

Tree component	Tree d.b.h., mm		
	76	152	228
	- - - - - Percent - - - - -		
Stem to apical tip	14.6	10.5	8.9
Live branches	46.8	37.1	29.4
Stump-root system	17.9	13.3	10.7

Latifolia Compared to Murrayana

Varietal differences in the characteristics reported here were not major, except as noted in the following paragraphs.

In the latitudes common to the two varieties (40, 42.5, and 45 degrees), branch diameter averaged 2 mm less in *murrayana* trees than in *latifolia*; at latitudes 40 and 42.5 degrees branch angle averaged 10 degrees larger on *murrayana* than on *latifolia* (85 vs. 75 degrees).

Latifolia bore significantly more cones than *murrayana* at all three latitudes. All of the *murrayana* trees were classified as open-coned, whereas 15 to 50 percent of the *latifolia* trees at these latitudes were classified as closed-coned (fig. 1-19).

Latifolia had about 20 percent thicker lateral rootbark than *murrayana*, and stumpbark was about 15 percent thicker on *latifolia* than on *murrayana*.

With diameter data pooled, *murrayana* had more live branchbark as a percentage of gross live branch volume than *latifolia*—42.6 percent vs. 38.0 percent.

1-16 REFERENCES

- Agee, James K. Fuel weights of understory-grown conifers in southern Oregon. *Canadian Journal of Forest Research*. 13(4): 648-656; 1983.
- Alden, John N.; Zasada, John. Potential of lodgepole pine as a commercial forest tree species on an upland site in interior Alaska. In: Murray, Mayo, ed. *Lodgepole pine: regeneration and management: Proceedings of a fourth international workshop*; 1982 August 17-19; Hinton, AB, Canada. General Technical Report PNW-157. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1983: 42-48.
- Alemdag, I. S. Stand volume tables for white spruce and lodgepole pine in the upper Liard River area, Yukon Territory. Information Report FMR-X-54 (Study FM-95). Ottawa, ON: Department of the Environment, Canadian Forestry Service, Forest Management Institute; 1973. 6 p.
- Alemdag, I. S. Metric site-index curves for white spruce and lodgepole pine in the upper Liard River area, Yukon Territory. Information Report FMR-X-33M. Ottawa, ON: Department of the Environment, Canadian Forestry Service, Forest Management Institute; 1976. 18 p.
- Alexander, Robert R. Silviculture of subalpine forests in the Central and Southern Rocky Mountains: the status of our knowledge. Research Paper RM-121. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1974. 88 p.
- Alexander, Robert R.; Tackle, David; Dahms, Walter G. Site indexes for lodgepole pine, with corrections for stand density: methodology. Research Paper RM-29. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1967. 18 p.
- Allen, Gerald M.; Adams, David L.; Houck, Geoffrey L.; Hatch, Charles R. Volume tables for small trees in northern Idaho. Station Note 27. Moscow, ID: University of Idaho, College of Forestry, Wildlife and Range Sciences, Forest, Wildlife and Range Experiment Station; 1976. 6 p.
- Amman, Gene D. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. Research Note INT-96. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1969. 8 p.
- Amman, Gene D. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology*. 65(1): 138-140; 1972.
- Amman, Gene D. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology*. 2(4): 541-547; 1973.
- Amman, Gene D.; Pace, Vincent E. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. Research Note INT-209. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1976. 8 p.
- Amman, Gene D.; Baker, Bruce H.; Stipe, Lawrence E. Lodgepole pine losses to mountain pine beetle related to elevation. Research Note INT-171. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1973. 8 p.
- Amman, Gene D.; McGregor, Mark D.; Cahill, Donn B.; Klein, William H. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. General Technical Report INT-36. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 19 p.
- Anderson, Tom D.; Tiedemann, Arthur R. Periodic variation in physical and chemical properties of two central Washington soils. Research Note PNW-125. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1970. 9 p.
- Armit, D. Miscellaneous notes: cone habit of lodgepole pine. In: *Forest research review year ended March 1964*. Victoria, BC: British Columbia Forest Service; 1964: 56-57.
- Armit, D. Silvics and silviculture of lodgepole pine in the north central interior of British Columbia. Research Note 40. Victoria, BC: Department of Lands, Forests, and Water Resources, British Columbia Forest Service; 1966. 50 p.
- Bagnell, C. Robert, Jr. Species distinction among pollen grains of *Abies*, *Picea*, and *Pinus* in the Rocky Mountain area (a scanning electron microscope study). *Review of Paleobotany and Palynology*. 19(3): 203-220; 1975.
- Bannan, M. W. Tracheid size and anticlinal divisions in the cambium of lodgepole pine. *Canadian Journal of Botany*. 42(9): 1105-1118; 1964.
- Barrett, James W.; Martin, Robert E.; Wood, Donald C. Northwestern ponderosa pine and associated species. In: Burns, Russell M., compiler. *Silvicultural systems for the major forest types of the United States*. Agriculture Handbook 445. Washington, DC: U.S. Department of Agriculture, Forest Service; 1983: 16-18.
- Barton, G. M. Western-conifer extractive chemistry aids the technologist. Information Report VP-X-142. Vancouver, BC: Department of the Environment, Canadian Forestry Service, Western Forest Products Laboratory; 1975. 18 p. Available from: Forintek Canada Corp., Vancouver, BC.
- Bates, C. G. The production, extraction, and germination of lodgepole pine seed. Technical Bulletin 191. Washington, DC: U.S. Department of Agriculture; 1930. 92 p.
- Bates, Carlos G. The biology of lodgepole pine as revealed by the behavior of its seed. *Journal of Forestry*. 15(4): 410-416; 1917.
- Bates, Carlos G. A key to the identification of some coniferous seedlings. *Journal of Forestry*. 23: 278-281; 1925.
- Benecke, U.; Morris, J. Y. Tree provenance trials. In: Orwin, Joanna, ed. *Revegetation in the rehabilitation of mountain lands: symposium proceedings*; 1974. F.R.I. Symposium. 16. Rotorua: New Zealand Forest Service, Forest Research Institute; 1978: 99-138.
- Berndt, Herbert W.; Gibbons, Robert D. Root distribution of some native trees and understory plants growing on three sites within ponderosa pine watersheds in Colorado. Station Paper 37. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1958. 14 p.

- Berry, A. B. Metric form-class volume tables. Information Report PI-X-10. Chalk River, ON: Canadian Forestry Service, Petawawa National Forestry Institute; 1981. 24 p.
- Berryman, Alan A. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environmental Entomology*. 5(6): 1225-1233; 1976.
- Berryman, Alan A. A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. In: Berryman, Alan A.; Amman, Gene D.; Stark, Ronald W., tech. eds., Kibbee, Darline L., publ. ed. The theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station; 1978: 98-105.
- Betts, H. S. Lodgepole pine (*Pinus contorta* var. *latifolia*). American Woods. Washington, DC: U.S. Department of Agriculture, Forest Service; 1945. 5 p.
- Birot, Par Y. Variabilité géographique du poids de la graine de *Pinus contorta*: Geographic variation in seed weight in *Pinus contorta*. *Silvae Genetica*. 27(1): 32-40; 1978.
- Bishop, Daniel M. Lodgepole pine rooting habits in the Blue Mountains of northeastern Oregon. *Ecology*. 43(1): 140-143; 1962.
- Blyth, A. W. Standard volume tables for lodgepole pine in Alberta. Technical Note 9. Ottawa, ON: Canada Department of Northern Affairs and Natural Resources, Forestry Branch, Forest Research Division; 1955. 14 p.
- Boggie, Robert. Effect of water-table height on root development of *Pinus contorta* on deep peat in Scotland. *Acta Oecologica Scandinavica*. 23(3): 304-312; 1972.
- Bonnor, G. M. The influence of stand density on the correlation of stem diameter with crown width and height for lodgepole pine. *Forestry Chronicle*. 40(3): 347-349; 1964.
- Bonnor, G. M. Aerial stand volume tables for ten forest types in Canada: Project S-1. Information Report FMR-X-1. Ottawa, ON: Department of Forestry Canada, Forest Management Research and Services Institute; 1966. [Pagination unknown.]
- British Columbia Forest Service. Volume, yield, and stand tables for some of the principal timber species of British Columbia. Victoria, BC: British Columbia Forest Service, Lands Department, Research Division; 1936. 53 p.
- Brown, James K. Fire cycles and community dynamics in lodgepole pine forests. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 429-456. (vol. 1).
- Brown, James K. Predicting crown weights for 11 Rocky Mountain conifers. In: Oslo biomass studies: IUFRO Congress; 1976 June: 103-115.
- Brown, James K. Weight and density of crowns of Rocky Mountain conifers. Research Paper INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1978. 56 p.
- Cabrera, Homero. Phloem structure and development in lodgepole pine. In: Berryman, Alan A.; Amman, Gene D.; Stark, Ronald W., tech. eds., Kibbee, Darline L., publ. ed. The theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station; 1978: 54-63.
- Cerezke, H. F. Bark thickness and bark resin cavities on young lodgepole pine in relation to *Hylobius warreni* Wood (Coleoptera:Curculionidae). *Canadian Journal of Forest Research*. 3(4): 599-601; 1973.
- Chapman, R. C.; Baldwin, V. C.; Clausnitzer, R. R. Cubic foot volume, bole green weight and total above ground green weight of small diameter lodgepole pine, larch and ponderosa pine. Research Bulletin XB 0914. Pullman, WA: Washington State University, Agricultural Research Center; 1982. 7 p.
- Christie, J. M.; Lines, R. A comparison of forest productivity in Britain and Europe in relation to climatic factors. *Forest Ecology and Management*. 2(2): 75-102; 1979.
- Clausen, Jens. Population studies of alpine and subalpine races of conifers and willows in the California high Sierra Nevada. *Evolution*. 19(1): 56-68; 1965.
- Cole, D. M.; Jensen, C. E. Estimating phloem thickness in lodgepole pine stands using electrical resistance measurements. *Canadian Journal of Forest Research*. 10(1): 102-106; 1980.
- Cole, Dennis M. A cubic-foot stand volume equation for lodgepole pine in Montana and Idaho. Research Note INT-150. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1971. 8 p.
- Cole, Dennis M. Estimation of phloem thickness in lodgepole pine. Research Paper INT-148. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1973. 10 p.
- Cole, Dennis M. Merchantable cubic stand volume conversion factors for lodgepole pine in Montana and Idaho. Research Note INT-259. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 12 p.
- Cole, Dennis M. Canopy development in lodgepole pine: implications for wildlife studies and multiple resource management. General Technical Report INT-139. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 13 p.
- Cole, Dennis M.; Edminster, Carleton B. Growth and yield of lodgepole pine. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. Lodgepole pine: the species and its management: symposium proceedings; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 263-290.
- Cole, Dennis M.; Jensen, Chester E. Models for describing vertical crown development of lodgepole pine stands. Research Paper INT-292. Ogden, UT: U.S. Department

- of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 10 p.
- Cole, Dennis M.; Stage, Albert R. Estimating future diameters of lodgepole pine trees. Research Paper INT-131. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1972. 20 p.
- Cole, Walter E. Interaction between mountain pine beetle and dynamics of lodgepole pine stands. Research Note INT-170. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1973. 6 p.
- Cole, Walter E.; Amman, Gene D. Mountain pine beetle dynamics in lodgepole pine forests. Part 1: course of an infestation. General Technical Report INT-89. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 56 p.
- Cole, Walter E.; Cahill, Donn B. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *Journal of Forestry*. 74(5): 294-297; 1976.
- Cooper, Robert W.; Schopmeyer, Clifford S.; McGregor, William H. Davis. Sand pine regeneration on the Ocala National Forest. Product Research Report 30. Washington, DC: U.S. Department of Agriculture, Forest Service; 1959. 37 p.
- Critchfield, W. B. A new hybrid Christmas tree. *Southern Lumberman*. 211(2632): 132-133; 1965.
- Critchfield, William B. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation Publication 3. Cambridge, MA: Harvard University; 1957. 118 p.
- Critchfield, William B. The genetics of lodgepole pine. Research Paper WO-37. Washington, DC: U.S. Department of Agriculture, Forest Service; 1980. 57 p.
- Crossley, D. I. The production and dispersal of lodgepole pine seed. Technical Note 25. Ottawa, ON: Canada Department of Northern Affairs and National Resources, Forestry Branch, Forest Research Division; 1955. 12 p.
- Crossley, D. I. Effect of crown cover and slash density on the release of seed from slash-borne lodgepole pine cones. Forest Research Division Technical Note 41. Ottawa, ON: Forestry Branch, Department of Northern Affairs and National Resources; 1956a. 51 p.
- Crossley, D. I. Fruiting habits of lodgepole pine. Technical Note 35. Ottawa, ON: Canada Department of Northern Affairs and National Resources, Forestry Branch, Forest Research Division; 1956b. 32 p.
- Cunningham, A.; Roberts, Q. A provenance trial of *Pinus contorta* at 4,800 ft. in the Kaweka Range. *New Zealand Journal of Forestry*. 15(1): 79-87; 1970.
- Dahms, Walter. Gross yield of central Oregon lodgepole pine. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 208-232. (vol. 1).
- Dahms, Walter G. Gross and net yield tables for lodgepole pine. Research Paper PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1964. 14 p.
- Dahms, Walter G. Relationship of lodgepole pine volume increment to crown competition factor, basal area, and site index. *Forest Science*. 12(1): 74-82; 1966.
- Dahms, Walter G. Growth and soil moisture in thinned lodgepole pine. Research Paper PNW-127. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1971a. 32 p.
- Dahms, Walter G. Fifty-five-year-old lodgepole pine responds to thinning. Research Note PNW-141. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1971b. 13 p.
- Davidsonia. *Pinus contorta* D. Douglas ex Loudon: shore pine, lodgepole pine. *Davidsonia*. 10(4): 75-83; 1979.
- Davies, E. J. M. Useless? The case against *contorta*. *Scottish Forestry*. 34(2): 110-113; 1980.
- Dietrichson, Jon. Geografisk variasjon hos *Pinus contorta* Dougl.: en undersøkelse med sikte på treslagets bruk i Norge: Geographic variation in *Pinus contorta* Dougl.: a study aiming at the use of the species in Norway. *Norske Skogforsoksvesen*. 28(2): 111-140; 1970.
- Dobie, J.; Middleton, G. R. Lumber yields from sweepy lodgepole pine. *Forestry Chronicle*. 56(2): 66-67; 1980.
- Dominion Forest Service. Interpolated volume tables (total volume) for use in compilation of sample plot data. Miscellaneous Series 3. Ottawa, ON: Dominion Forest Service; 1944. 20 p.
- Drake, Erik. Undersökning av barkvolymen i södra och mellersta Sverige: A study of the bark volume in south and central Sweden. Report 149. Uppsala, Sweden: The Swedish University of Agricultural Sciences, Department of Forest Products; 1983. 61 p. plus appendixes.
- Duff, G. Estimation of volume of forked trees in exotic coniferous stands in New Zealand. Forest Research Note 6. Wellington: Ministry of Forests, New Zealand Forest Service, Forest Research Institute; 1956. 10 p.
- Duff, G. Yield tables for unthinned stands of the "green" varieties of *Pinus contorta* in New Zealand. Technical Paper 50. Wellington: New Zealand Forest Service, Forest Research Institute; 1966. 37 p.
- Duffy, Patrick J. B.; Meyer, Merle P. A preliminary study of aerial volume table construction for lodgepole pine in west-central Alberta. *Forestry Chronicle*. 38(2): 212-218; 1962.
- Dunsworth, B. G.; Northway, S. M.; Packee, E. C. Shore pine and Douglas-fir height and volume development on low productivity sites. *Canadian Journal of Forest Research*. 12(2): 438-439; 1982.
- Dykstra, Gary F. Drought resistance of lodgepole pine seedlings in relation to provenance and tree water potential. Research Note 62. Victoria, BC: British Columbia Forest Service, Research Division; 1974. 7 p.
- Edminster, Carleton B. RMYLD: computation of yield tables for even-aged and two-storied stands. Research Paper RM-199. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1978. 26 p.
- Edwards, M. V. A summary of information on *Pinus contorta* with special reference to its use in Europe. Part 1. *Forestry Abstracts*. 15(4): 389-396; 1954.

- Edwards, M. V. A summary of information on *Pinus contorta* with special reference to its use in Europe. Part II. Forestry Abstracts. 16(1): 3-13; 1955.
- Eis, S.; Craigdallie, D.; Simmons, C. Growth of lodgepole pine and white spruce in the central interior of British Columbia. Canadian Journal of Forest Research. 12(3): 567-575; 1982.
- Eriksson, Harry. Volymfunktioner for stamde trad av ask, asp, klipbal och contorta-tall: Tree volume functions for ash, aspen, alder and lodgepole pine in Sweden. (*Fraxinus excelsior* L., *Populus tremula* L., *Alnus glutinosa* (L.) Gartn., *Pinus contorta* Dougl. var. *latifolia* Engelm.). Research Note 26. Stockholm, Sweden: Royal College of Forestry; 1973. 26 p.
- Fahnestock, George R. Logging slash flammability. Research Paper 58. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1960. 67 p.
- Faurot, James L. Estimating merchantable volume and stem residue in four timber species: ponderosa pine, lodgepole pine, western larch, Douglas-fir. Research Paper INT-196. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 55 p.
- Fitzsimons, B. An investigation of the effects of poor stem form and sawmill recovery on coastal lodgepole pine. Irish Forestry. 39(1): 30-47; 1982.
- Forestry Research West. Relative ecological position and extent of occurrence of major species. Forestry Research West. [Fort Collins, CO]: U.S. Department of Agriculture, Forest Service; 1983 June. Cover illustration.
- Forrest, G. I. Geographical variation in the monoterpenes of the resin of *Pinus contorta*. In: Seals, D. T., chairman, [and others]. EEC symposium on forest tree biochemistry: proceedings; 1977 January 25-27; Brussels. Luxembourg: Commission of the European Communities; 1977a: 55-71.
- Forrest, G. I. Identification of unknown lodgepole pine origins. Research Information Note 30/77/GEN. Surrey, England: Forestry Commission Research and Development Division, Forestry Commission Research Station; 1977b. 4 p.
- Forrest, G. I. Monoterpene variation in lodgepole pine (*Pinus contorta*) and Scots pine (*Pinus sylvestris*). In: Rudin, Dag, ed. Proceedings of the conference on biochemical genetics of forest trees; 1978; Umea, Sweden. Report 1. Umea, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology; 1979: 136-150.
- Forrest, G. Ian. Geographical variation in oleoresin monoterpene composition of *Pinus contorta* from natural stands and planted seed collections. Biochemical Systematics and Ecology 9(2/3): 97-103; 1981.
- Fosberg, F. R. *Pinus contorta* and its variations. Bailey. 7(1): 7-10; 1959.
- Franklin, E. C.; Callaham, R. Z. Multinodality, branching and forking in lodgepole pine (*Pinus contorta* var. *murrayana* Engelm.). Silvae Genetica. 19(5/6): 180-184; 1970.
- Franklin, Edward Carlyle. An analysis of branching and forking characteristics in families of lodgepole pine (*Pinus contorta* var. *murrayana* Engelm.). Berkeley, CA: University of California; 1964. 79 p. M.S. thesis.
- Gail, Floyd W.; Long, E. M. A study of site, root development, and transpiration in relation to the distribution of *Pinus contorta*. Ecology. 16: 88-100; 1935.
- Gary, Howard L. Canopy weight distribution affects wind-speed and temperature in a lodgepole pine forest. Forest Science. 20(4): 369-371; 1974.
- Gary, Howard L. Crown structure and distribution of biomass in a lodgepole pine stand. Research Paper RM-165. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1976. 20 p.
- Gary, Howard L. The vertical distribution of needles and branchwood in thinned and unthinned 80-year-old lodgepole pine. Northwest Science. 52(4): 303-309; 1978.
- Gilbertson, R. L.; Leaphart, C. D.; Johnson, F. D. Field identification of roots of conifers in the Inland Empire. Forest Science. 7(4): 352-356; 1961.
- Griffin, James R.; Critchfield, William B. The distribution of forest trees in California. Research Paper PSW-82. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1972 (reprinted with supplement 1976). 118 p.
- Guernsey, F. W.; Dobie, J. Properties and utilization of lodgepole pine in western Canada. Department of Forestry Publication 1143. Ottawa, ON: Minister of Forestry, Canada Department of Forestry; 1966. 24 p.
- Gunther, A. Everard. The twisting of the tamarac pine. Scottish Forestry Journal. 43(2): 81-94; 1929.
- Hagner, Mats. Geographic variation in *Pinus contorta* and *Picea mariana* with respect to cone size, seedling growth rhythm and cotyledons. In: *Pinus contorta* as an exotic species: proceedings of the IUFRO working party meeting 1980 on *Pinus contorta* provenances (S2-02-06) in Norway and Sweden. Svergis Lantbruksuniversitet Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics; 1980a: 83-101.
- Hagner, Mats. Geographic variation in seed quality of lodgepole pine (*Pinus contorta* Dougl.) between and within stands. In: *Pinus contorta* as an exotic species: proceedings of the IUFRO working party meeting 1980 on *Pinus contorta* provenances (S2-02-06) in Norway and Sweden. Svergis Lantbruksuniversitet Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics; 1980b: 275-286.
- Hakkila, Pentti; Panhelainen, Arja. On the wood properties of *Pinus contorta* in Finland. Communicationes Instituti Forestalis Fenniae. 73(1); 1970. 43 p.
- Hamilton, G. J.; Christie, J. M. Forest management tables (metric). Forestry Commission Booklet 34. London: Forestry Commission; 1971. 201 p.
- Hanan, A. M. S. "Bolander's pine?" Irish Forestry. 20(1): 3-6; 1963.
- Hansen, Barbara S.; Cushing, Edward J. Identification of pine pollen of late Quaternary age from the Chuska Mountains, New Mexico. Geological Society of America Bulletin. 84(4): 1181-1200; 1973.
- Hanzlik, Edward J. A growth and volume study of lodgepole pine in the Ochoco Mountains. University of Washington Forestry Club Annual 4: 27-33; 1916.

- Harris, J. Maddern. Physical properties, resin content, and tracheid length of lodgepole pine grown in New Zealand. *New Zealand Journal of Forest Science*. 3(1): 91-109; 1973.
- Hartl, Daniel L. Selection for serotiny in lodgepole pine: mathematical analysis of the model of Perry and Lotan. *Evolution*. 33(3): 969-972; 1979.
- Hawksworth, Frank G. Upper altitudinal limits of lodgepole pine dwarfmistletoe in the Central Rocky Mountains. *Phytopathology*. 46(10): 561-562; 1956.
- Hawksworth, Frank G.; Lister, C. Kendall; Cahill, Donn B. Phloem thickness in lodgepole pine: its relationship to dwarf mistletoe and mountain pine beetle (Coleoptera: Scolytidae). *Environmental Entomology*. 12(5): 1447-1448; 1983.
- Heger, L. A trial of Hohenadl's method of stem form and stem volume estimation. *Forestry Chronicle*. 41(4): 466-475; 1965.
- Hellum, A. K.; Barker, N. A. Cone moisture content influences seed release in lodgepole pine. *Canadian Journal of Forest Research*. 10(3): 239-244; 1980.
- Hellum, A. K.; Barker, N. A. The relationship of lodgepole pine cone age and seed extractability. *Forest Science*. 27(1): 62-70; 1981.
- Hellum, A. K.; Pelchat, M. Temperature and time affect the release and quality of seed from cones of lodgepole pine from Alberta. *Canadian Journal of Forest Research*. (2): 154-159; 1979.
- Henderson, J.; Petty, J. A. A comparison of wood properties of coastal and interior provenances of lodgepole pine. *Forestry*. 45(1): 49-57; 1972.
- Hobbs, Stephen D.; Partridge, Arthur D. Wood decays, root rots, and stand composition along an elevation gradient. *Forest Science*. 25(1): 31-42; 1979.
- Honer, T. G. Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada. Information Report FMR-X-5. Ottawa, ON: Canada Department of Forestry and Rural Development, Forestry Branch, Forest Management Research and Services Institute; 1967. [Pagination unknown.]
- Hornibrook, E. M. Cubic-foot volume table for lodgepole pine. Research Note 4. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1948. 3 p.
- Hornibrook, E. M. Estimating defect in mature and over-mature stands of three Rocky Mountain conifers. *Journal of Forestry*. 48(9): 408-417; 1950.
- Horton, K. W. Rooting habits of lodgepole pine. Technical Note 67. Ottawa, ON: Canada Department of Northern Affairs and National Resources, Forestry Branch, Forest Research Division; 1958. 26 p.
- Hosie, R. C. Lodgepole pine. In: *Native trees in Canada*. [Ottawa]: Canadian Forestry Service, Department of the Environment; 1973: 52-53.
- Illingworth, K. Variation in *Pinus contorta* with particular reference to British Columbia. In: *Forest research review: year ended March, 1969*. Victoria, BC: British Columbia Forest Service, Department of Lands, Forests, and Water Resources, Forest Research Division; 1969: 42-46.
- Illingworth, K. Geographic variation in *Pinus contorta*. In: *Proceedings 13th meeting on forest tree breeding in Canada*; 1971: 107-112.
- Illingworth, Keith. Natural variation within lodgepole pine in British Columbia. In: *Meeting of IUFRO working party on Pinus contorta provenance*; 1974 September; Edinburgh, Scotland. Research and Development Paper 114. United Kingdom: Forestry Commission of Great Britain; 1976: 40-43.
- Jeffers, J. N. R.; Black, T. M. An analysis of variability in *Pinus contorta*. *Forestry*. 36(2): 199-218; 1963.
- Jeffers, J. N. R.; Spragg, L. K. A volume table for lodgepole pine (*Pinus contorta* Loudon). Statistics Section Paper 127. London: Forestry Commission; 1966. 2 p.
- Jenny, H.; Arkley, R. J.; Schultz, A. M. The pygmy forest-podsol ecosystem and its dune associates of the Mendocino coast. *Madroño*. 20(2): 60-74; 1969.
- Johnson, Floyd. Volume tables for lodgepole pine in Oregon and Washington based on diameter, height and form. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1952. 32 p.
- Johnson, F. A., compiler. Volume tables for Pacific Northwest trees (a compilation). Agriculture Handbook 92. Washington, DC: U.S. Department of Agriculture, Forest Service; 1955. 112 p.
- Johnstone, W. D. Variable stand density yields of natural lodgepole pine stands in Alberta. In: Baumgartner, David M., ed. *Management of lodgepole pine ecosystems: symposium proceedings*; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 186-207. (vol. 1).
- Johnstone, W. D. Variable-density yield tables for natural stands of lodgepole pine in Alberta. Forestry Technical Report 20. Ottawa, ON: Department of Fisheries and the Environment, Canadian Forestry Service, Northern Forest Research Centre; 1976. 110 p.
- Jonsson, Alena; Eriksson, Gösta; Dormling, Ingegerd; Ifver, Jan. Studies on frost hardiness of *Pinus contorta* Dougl. seedlings grown in climate chambers. *Studia Forestalia Suecica* 157. Uppsala, Sweden: Swedish University of Agricultural Sciences, College of Forestry; 1981. 47 p.
- Kamra, S. K. Seed biology of lodgepole pine (*Pinus contorta* Dougl.). Report 3. Umea, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology; 1982. 51 p.
- Kellogg, R. M.; Rowe, S.; Koeppen, R. C.; Miller, R. B. Identification of the wood of the soft pines of western North America. *IAWA Bulletin n.s.* 3(2): 95-101; 1982.
- Kimes, D. S.; Smith, J. A.; Berry, J. K. Extension of the optical diffraction analysis technique for estimating forest canopy geometry. *Australian Journal of Botany*. 27(5): 575-588; 1979.
- Knapp, Allan K.; Anderson, Jay E. Effect of heat on germination of seeds from serotinous lodgepole pine cones. *American Midland Naturalist*. 104(2): 370-372; 1980.
- Knowles, Margaret Helen. Genetic variation of lodgepole pine over time and microgeographical space. Dissertation Abstracts International. 41(4): 1206-B; 1980. Abstract.

- Knowles, Peggy; Grant, Michael C. Genetic variation of lodgepole pine over time and microgeographical space. Evolution; [in press]. 30 p.
- Koch, Peter. Utilizing lodgepole pine forests of the 21st century—a research program. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. Lodgepole pine: the species and its management: symposium proceedings; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 343-349.
- Kotok, E. S. Tree characteristics influence 2 × 4 stud yield of lodgepole pine. Research Note INT-63. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1967. 8 p.
- Kotok, E. S. Lodgepole pine (*Pinus contorta* Dougl.). American Woods FS 253 (rev.). Washington, DC: U.S. Department of Agriculture, Forest Service; 1971. 7 p.
- Kovalchik, Bernard; Blake, George. The effect of piling and burning versus chopping of logging residues on natural regeneration of serotinous lodgepole pine forests. Research Note 11. Missoula, MT: University of Montana, School of Forestry, Montana Forest and Conservation Experiment Station; 1972. 4 p.
- Kozak, A.; Yang, R. C. Equations for estimating bark volumes and thickness of commercial trees in British Columbia. Forestry Chronicle. 57(3): 112-115; 1981.
- Krajina, V. J. Ecology of forest trees in British Columbia. Ecology of Western North America. 2: 1-146; 1970.
- Kumler, M. L. Plant succession on the sand dunes of the Oregon coast. Ecology. 50(4): 695-704; 1969.
- Laing, E. V. Morphological variations in tree species. In: Report on forest research for the year ending March, 1954. London: Forestry Commission; 1955: 56-57.
- Lange, Robert W. Bark thickness, *k*, factors for four Montana coniferous tree species. Research Note 9. Missoula, MT: University of Montana, School of Forestry, Montana Forest and Conservation Experiment Station; 1971. 2 p.
- La Roi, George H.; Hnatiuk, Roger J. The *Pinus contorta* forests of Banff and Jasper National Parks: a study in comparative synecology and syntaxonomy. Ecological Monographs. 50(1): 1-29; 1980.
- Larson, Larry L. Vegetative variability along a gradient from lodgepole pine—spruce-fir. Fort Collins, CO: Colorado State University; 1978. 101 p. Ph.D. dissertation. Available from: University Microfilms International, Ann Arbor, MI.
- Lindgren, Dag; Krutzsch, Peter; Twetman, Jan; Kiellander, Carl Ludvig. Survival and early growth of *Pinus contorta* provenances in northern Sweden. Research Note 20. Stockholm: Royal College of Forestry, Department of Forest Genetics; 1976. 42 p.
- Lines, R.; Mitchell, A. F.; Pearce, M. L. Provenance: lodgepole pine, Scots pine, Sitka spruce, silver firs, Douglas fir. In: Report on forest research for the year ended March 1971. London: Forestry Commission; 1971: 39-44.
- Lines, Roger; Booth, T. C. Investigation of basal sweep of lodgepole and shore pines in Great Britain. Forestry (Great Britain). 45(1): 59-66; 1972.
- Linhart, Yan B. Maintenance of variation in cone morphology in California closed-cone pines: the roles of fire, squirrels and seed output. Southwestern Naturalist. 23(1): 29-40; 1978.
- Little, Elbert L., Jr. Eight pine species at Onion Valley, California. Leaflet Western Botany. 10(15): 289-292; 1966.
- Little, Elbert L., Jr. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. Miscellaneous Publication 1146. Washington, DC: U.S. Department of Agriculture, Forest Service; 1971.
- Longyear, B. O. The evergreen trees of Colorado. Bulletin 130. Fort Collins, CO: Colorado Agricultural College, Agricultural Experiment Station; 1908. 32 p.
- Loope, Lloyd L. Dynamics of forest communities in Grand Teton National Park. Naturalist. 22(1): 39-47; 1971.
- Lotan, James E. Sampling serotinous cones in lodgepole pine. Proceedings Montana Academy of Science. 23: 20-24; 1963.
- Lotan, James E. Regeneration of lodgepole pine: a study of slash disposal and cone opening. Research Note INT-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1964. 4 p.
- Lotan, James E. Cone serotiny of lodgepole pine near West Yellowstone, Montana. Forest Science. 13(1): 55-59; 1967.
- Lotan, James E. Cone serotiny of lodgepole pine near Island Park, Idaho. Research Paper INT-52. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1968. 6 p.
- Lotan, James E. Regeneration of lodgepole pine forests in the Northern Rocky Mountains. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975a: 516-535. (vol. 2).
- Lotan, James E. The role of cone serotiny in lodgepole pine forests. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975b: 471-495. (vol. 1).
- Lotan, James E. Cone serotiny—fire relationships in lodgepole pine. In: Tall Timbers fire ecology conference 14 and Intermountain Fire Research Council fire and land management symposium: proceedings; 1974 October 8-10; Missoula, MT. Tallahassee, FL: Tall Timbers Research Station; 1976: 267-278.
- Lotan, James E.; Alexander, Robert R. Lodgepole pine. In: Silvicultural systems for the major forest types of the United States. Agriculture Handbook 445. Washington, DC: U.S. Department of Agriculture, Forest Service, Division of Timber Management Research; 1973: 42-44.
- Lotan, James E.; Critchfield, William B. Silvics of *Pinus contorta*. In: Silvics of North American species. Agriculture Handbook. Washington, DC: U.S. Department of Agriculture, Forest Service; [in press].

- Lotan, James E.; Jensen, Chester E. Estimating seed stored in serotinous cones of lodgepole pine. Research Paper INT-83. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1970. 10 p.
- Lotan, James E.; Perry, David A. Ecology and regeneration of lodgepole pine. Agriculture Handbook 606. Washington, DC: U.S. Department of Agriculture, Forest Service; 1983. 51 p.
- Lotan, James Elmer. Cone serotiny in *Pinus contorta*. Ann Arbor, MI: University of Michigan; 1970. 94 p. Ph.D. dissertation.
- Macaulay, James Donald. Mechanical seed extraction of lodgepole pine. Dissertation Abstracts International. 36(12, Part 1): 6278B-6279B; 1976. Abstract.
- MacDonald, J.; Wood, R. F. *Pinus contorta* Loudon. In: MacDonald, James; Wood, R. F.; Edwards, M. V.; Aldhous, J. R., eds. Exotic forest trees in Great Britain. Forestry Commission Bulletin 30. London: Forestry Commission; 1957: 94-100.
- Mack, Richard N. Pollen size variation in some western North American pines as related to fossil pollen identification. Northwest Science. 45(4): 257-269; 1971.
- MacLean, Colin; Berger, John M. Softwood tree volume equations for major California species. Research Note PNW-266. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1976. 34 p.
- Malcolm, F. B. Sacrificing short butt log to chips may reduce lodgepole stud warping. Forest Industries. 95(5): 88-89; 1968.
- Manning, T. D. R.; Hemmingson, J. A. Bark and oleoresin monoterpene hydrocarbons of *Pinus contorta* grown in New Zealand. New Zealand Journal of Science. 18: 115-118; 1975.
- Maschnig, E. [Variation of cotyledon number in some *Pinus contorta* provenances.] In German. Silvae Genetica. 20(1/2): 10-14; 1971.
- Massie, M. R. C.; Manning, G. H.; McCloskey, K. R. Metric single-tree total volume tables for the Yukon Territory. Information Report BC-X-242. Victoria, BC: Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre; 1983. 19 p.
- Matthews, J. D. Some applications of genetics and physiology in thinning. Forestry (Great Britain). 36(2): 172-180; 1963.
- Mayer, Kenneth E.; Fox, Lawrence, III. Identification of conifer species groupings from Landsat digital classifications. Journal of the American Society of Photogrammetry. 48(11): 1607-1614; 1981.
- McDougal, Fred W. The importance of lodgepole pine in Canada. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 10-26. (vol. 1).
- McMillan, Calvin. The edaphic restriction of *Cupressus* and *Pinus* in the coast ranges of central California. Ecological Monographs. 26(3): 177-212; 1956.
- McMillan, Calvin. Survival of transplanted *Cupressus* and *Pinus* after thirteen years in Mendocino County, California. Madroño. 17(8): 250-253; 1964.
- McMullan, E. E.; Colangeli, A. Comparison of starch and polyacrylamide gel-electrophoresis and isoelectric focusing for isozyme analysis in two conifers. Silva Fennica. 16(2): 226-231; 1982.
- Ministry of Technology. Wood structure: home-grown timber investigations: lodgepole pine. In: Forest Products Research 1964. London: Ministry of Technology; 1965: 9.
- Mirov, N. T. Lodgepole pine discovered and misnamed. Madroño. 12: 156-157; 1954a.
- Mirov, Nicholas T. Geography of the genus *Pinus*. Bulletin of the Geological Society of America. 65(12/2): 1397; 1954b. Abstract.
- Moessner, Karl E. Preliminary aerial volume tables for conifer stands in the Rocky Mountains. Research Paper 41. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1957. 17 p.
- Moeur, Melinda. Crown width and foliage weight of Northern Rocky Mountain conifers. Research Paper INT-283. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 14 p.
- Mogren, E. W. Height growth in relation to crown size in juvenile lodgepole pine. Research Note 17. Fort Collins, CO: Colorado State University, College of Forestry and Natural Resources; 1967. 2 p.
- Moore, M. B. Seed source variation in lodgepole pine and 1st-year root development. Tree Planters' Notes. 32(4): 5-8; 1981a.
- Moore, Musser Beighley. Geographic variation in lodgepole pine in the Central Rocky Mountains. Fort Collins, CO: Colorado State University; 1981b. 188 p. Ph.D. dissertation. Available from: University Microfilms International, Ann Arbor, MI.
- Moss, Alan. Lodgepole pine in the Okanagan Valley. Scottish Forestry. 9(2): 68-72, 67; 1955.
- Moss, Alan. An investigation of basal sweep of lodgepole and shore pines in Britain. Forestry (Great Britain). 44(1): 43-65; 1971.
- Mowat, Edwin L. No serotinous cones on central Oregon lodgepole pine. Journal of Forestry. 58: 118-119; 1960.
- Muir, Patricia S. Final report: fire frequency and the life history of lodgepole pine (*Pinus contorta* var. *latifolia*). Madison, WI: University of Wisconsin, Department of Botany; 1982. 33 p.
- Muir, Patricia S.; Lotan, James E. Serotiny and life history of *Pinus contorta* var. *latifolia*. Canadian Journal of Botany. 63: 938-945; 1985.
- Muller, Robert A. Transmission components of solar radiation in pine stands in relation to climatic and stand variables. Research Paper PSW-71. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1971. 13 p.
- Myers, Clifford A. Taper tables, bark thickness, and diameter relationships for lodgepole pines in Colorado and Wyoming. Research Note RM-31. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1964a. 6 p.

- Myers, Clifford A. Volume tables and point-sampling factors for lodgepole pine in Colorado and Wyoming. Research Paper RM-6. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1964b. 16 p.
- Myers, Clifford A. Height-diameter curves for tree species subject to stagnation. Research Note RM-69. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1966. 2 p.
- Myers, Clifford A. Yield tables for managed stands of lodgepole pine in Colorado and Wyoming. Research Paper RM-26. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1967. 20 p.
- Myers, Clifford A. Board-foot volumes to a 6-inch top for lodgepole pines in Colorado and Wyoming. Research Note RM-157. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1969. 3 p.
- Neustein, S. A. Trial plantations at high elevations. In: Report on forest research for the year ended March 1965. London: Forestry Commission; 1966: 169-172.
- Newman, K. W.; Jancey, R. C. Sample size in studies of geographic variation. Canadian Journal of Botany. 59(11): 2158-2159; 1981.
- Nielsen, Carl Christian Norgard. En stabilitetsundersøgelse i *Pinus contorta* ved hjælp af en traekmålings metode: A stability study of *Pinus contorta* using a tensile force measurement method. Dansk Skovforenings Tidsskrift. 67(1): 1-41; 1982.
- Nilsson, Jan-Erik. Flowering in *Pinus contorta*. Sveriges Lantbruksuniversitet Report 2. Umea, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology; 1981. 128 p.
- Nyland, Edo. Lodgepole pine in the Yukon. In: *Pinus contorta* as an exotic species: proceedings of the IUFRO working party meeting 1980 on *Pinus contorta* provenances (S2-02-06) in Norway and Sweden. Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics; 1980: 27-43.
- O'Driscoll, J. *Pinus contorta* in Ireland. In: Proceedings of IUFRO joint meeting of working parties: lodgepole pine, Sitka spruce and *Abies* provenances [S2-02-06, S2-02-12 and S2-02-14]; 1978; Vancouver, Canada. Victoria, BC: British Columbia Ministry of Forests, Information Services Branch; 1978: 137-139. (vol. 2).
- O'Driscoll, J. The importance of lodgepole pine in Irish forestry. Irish Forestry. 37(1): 7-22; 1980.
- Oregon State Board of Forestry. Standard volume table for lodgepole pine on the Deschutes Plateau, Oregon. Salem, OR: Oregon State Board of Forestry; n.d. 1 p.
- Parker, H. A. Bark thickness of lodgepole pine. Silviculture Leaflet 49. Ottawa, ON: Department of Resources and Development, Forestry Branch, Division of Forest Research; 1950 November. 2 p. [Replaces Silviculture Leaflet 49 issued 1950 September.]
- Paul, Benson, H. Properties and uses of western pine. Wood Workers Digest. 64(1): 43-45; 1962.
- Peattie, Donald Culross. Beach and lodgepole pine. Natural History. 61(8): 372-378; 1952.
- Pederick, L. A. Provenance variation in *Pinus contorta*. In: Forestry Technical Paper 28. Melbourne, Australia: Forests Commission Victoria; 1980: 32-40.
- Perry, David A.; Lotan, James E. Variation in lodgepole pine (*Pinus contorta* var. *latifolia*): greenhouse response of wind pollinated families from five populations to day length and temperature—soil. Canadian Journal of Forest Research. 8(1): 81-89; 1978.
- Perry, David A.; Lotan, James E. A model of fire selection for serotiny in lodgepole pine. Evolution. 33(3): 958-968; 1979.
- Perry, David Anthony. Ecotypic variation in *Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine). Dissertation Abstracts International. 35(9): 4427-B; 1975. Abstract.
- Peterson, Glenn W.; Harvey, George M. Dispersal of *Scirrhia* (*Dothistroma*) *pini* conidia and disease development in a shore pine plantation in western Oregon. Plant Disease Reporter. 60(9): 761-764; 1976.
- Pfeifer, A. R. Factors that contribute to basal sweep in lodgepole pine. Irish Forestry. 39(1): 7-16; 1982.
- Pfister, Robert D.; Daubenmire, R. Ecology of lodgepole pine (*Pinus contorta* Dougl.). In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 27-46. (vol. 1).
- Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. Forest habitat types of Montana. General Technical Report INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 174 p.
- Plank, Marlin E.; Cahill, James M. Estimating cubic volume of small diameter tree-length logs from ponderosa and lodgepole pine. Research Note PNW-417. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1984. 7 p.
- Polge, Hubert. [The quality of wood of the principal exotic conifers used in French plantations.] In French. Annales de L'Ecole Nationale des Eaux et Forêts 20(3): 401-469; 1963.
- Quintus, Dick. Board foot volume table for lodgepole pine. Bend, OR: Oregon State Board of Forestry; 1951. 2 p. Mimeographed.
- Raile, Gerhard K. Estimating stump volume. Research Paper NC-224. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station; 1982. 4 p.
- Rehfeldt, G. E. Adaptation of *Pinus contorta* populations to heterogeneous environments in northern Idaho. Canadian Journal of Forest Research. 13(3): 405-411; 1983.
- Rehfeldt, G. E.; Wykoff, W. R. Periodicity in shoot elongation among populations of *Pinus contorta* from the Northern Rocky Mountains. Annals of Botany. 48: 371-377; 1981.
- Rehfeldt, Gerald E. Cold acclimation in populations of *Pinus contorta* from the Northern Rocky Mountains. Botanical Gazette. 141(4): 458-463; 1980.
- Reid, Collins Nurseries, Ltd. The management and silviculture of lodgepole pine in B.C. Occasional Paper 1.

- [Victoria, BC]: Forest Research Council of British Columbia; 1983. 64 p.
- Righter, F. I.; Stockwell, Palmer. The fertile species hybrid, *Pinus Murray-banksiana*. *Madroño*. 10(3): 65-69; 1949.
- Roche, L. Variation in lodgepole pine with reference to provenances planted in Great Britain and Ireland. *Forestry*. 39(1): 30-39; 1966.
- Roche, Laurence. The shore variety of *Pinus contorta*. *Baileya*. 11(1): 11-14; 1963.
- Safranyik, Les. Effects of climate and weather on mountain pine beetle populations. In: Berryman, Alan A.; Amman, Gene D.; Stark, Ronald W., tech. eds., Kibbee, Darline L., publ. ed. The theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station; 1978: 77-84.
- Satterlund, Donald R. Climatic factors and lodgepole pine. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 297-309. (vol. 1).
- Schmidt, W. C. Forests of the Rocky Mountain west. In: Lotan, James E.; Alexander, Martin E.; Arno, Stephen F.; [and others]. Effects of fire on flora. General Technical Report WO-16. Washington, DC: U.S. Department of Agriculture, Forest Service; 1981: 11-16.
- Schroeder, James G.; Phillips, Douglas R. Effect of sweep and crook on veneer yield. *Forest Products Journal*. 34(10): 45-47; 1984.
- Scott, D. Comparison between lodgepole pine and mountain beech in establishment and CO₂ exchange. *New Zealand Journal of Botany*. 8(3): 357-360; 1970.
- Shepperd, Wayne D.; Alexander, Robert R. Overview to silvicultural systems in the Central Rocky Mountains. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1983. 31 p.
- Shirling, A. E. The age of needle leaves. *Transactions of the Kansas Academy of Science*. 49(2): 161-166; 1946.
- Shrimpton, D. M.; Thomson, A. J. Growth characteristics of lodgepole pine associated with the start of mountain pine beetle outbreaks. *Canadian Journal of Forest Research*. 13: 137-143; 1983.
- Smith, Frederick Walter. Effects of competition for soil water on growth and water status of *Pinus contorta* on pumice soil. Seattle, WA: University of Washington; 1981. 142 p. Ph.D. dissertation. Available from: University Microfilms International, Ann Arbor, MI.
- Smith, J. H. G.; Ker, J. W. Timber volume depends on D²H. *British Columbia Lumberman*. 41(9): 28-30; 1957.
- Smith, J. H. G.; Kozak, A. Thickness, moisture content, and specific gravity of inner and outer bark of some Pacific Northwest trees. *Forest Products Journal*. 21(2): 38-40; 1971.
- Smith, J. Harry G. Root spread can be estimated from crown width of Douglas fir, lodgepole pine, and other British Columbia tree species. *Forestry Chronicle*. 40(4): 456-473; 1964.
- Smith, J. Harry G.; Bailey, Gordon R. Influence of stocking and stand density on crown widths of Douglas fir and lodgepole pine. *Commonwealth Forestry Review*. 43(3): 243-246; 1964.
- Smith, R. B. Development of dwarf mistletoe (*Arceuthobium*) infections on western hemlock, shore pine, and western larch. *Canadian Journal of Forest Research*. 1(1): 35-42; 1971.
- Smith, Richard H. Monoterpenes of lodgepole pine xylem resin: a regional study in Western United States. *Forest Science*. 29(2): 333-340; 1983.
- Smithers, L. A. Lodgepole pine in Alberta. Bulletin 127. Ottawa, ON: Canada Department of Northern Affairs and National Resources, Department of Forestry; 1961. 153 p.
- Snell, J. A. Kendall; Max, Timothy A. Bark-to-wood ratios for logging residue in Oregon, Washington, and Idaho. Administrative Report. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1982. 9 p.
- Spada, Benjamin. Estimating past diameters of several species in the ponderosa pine subregion of Oregon and Washington. Research Note 181. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1960. 4 p.
- Spalt, Karl W.; Reifsnnyder, William E. Bark characteristics and fire resistance: a literature survey. Occasional Paper 193. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station; 1962. 19 p.
- Sterba, Hubert. Stem curves—a review of the literature. *Forestry Abstracts*. 41(4): 141-145; 1980.
- Stock, Mary W.; Guenther, Jerry D.; Pitman, Gary B. Implications of genetic differences between mountain pine beetle populations to integrated pest management. In: Berryman, Alan A.; Amman, Gene D.; Stark, Ronald W., tech. eds., Kibbee, Darline L., publ. ed. The theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station; 1978: 197-201.
- Struble, G. R. Insect enemies in the natural control of the lodgepole needle miner. *Journal of Economic Entomology*. 60(1): 225-228; 1967.
- Struble, George R. Needle miner infestations in lodgepole pine east of the Sierra crest. Research Note PSW-177. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1968. 2 p.
- Sutherland, J. R.; Lock, W.; Woods, T. A. D.; Suttill, T. *Sirococcus* blight not seed-borne on serotinous lodgepole pine. *Canadian Forestry Service Research Notes*. 2(3): 20-22; 1982.
- Swan, E. P. Chemical methods of differentiating the wood of several western conifers. *Forest Products Journal*. 16(1): 51-54; 1966.
- Swan, H. S. D. Foliar nutrient concentrations in lodgepole pine as indicators of tree nutrient status and fertilizer requirement. Woodlands Report WR/42. Pointe Claire, PQ: Pulp and Paper Research Institute of Canada; 1972. 19 p.

- Tackle, David. Silvics of lodgepole pine. Miscellaneous Publication 12. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1959. 24 p.
- Taylor, Fred W.; Wang, Eugene I. C.; Micko, Michael M. Differences in the wood of lodgepole pine in Alberta. *Wood and Fiber*. 14(4): 296-309; 1982.
- Teich, A. H. Cone serotiny and inbreeding in natural populations of *Pinus banksiana* and *Pinus contorta*. *Canadian Journal of Botany*. 48(10): 1805-1809; 1970.
- Thiers, H. D.; Smith, A. H. A new species of *Suillus*. *Mycologia*. 65(6): 1375-1377; 1973.
- Thompson, C. F. Drag scarification trials in lodgepole pine logging slash in the Nelson Forest District of British Columbia (E.P. 714). Research Note 82. Victoria, BC: Ministry of Forests, Forest Service Research Division; 1978. 13 p.
- Tower, Gordon E. A study of the reproductive characteristics of lodgepole pine. *Proceedings Society of American Foresters*. 4(1): 84-106; 1909.
- Trappe, James M.; Harris, Robert W. Lodgepole pine in the Blue Mountains of northeastern Oregon. Research Paper 30. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1958. 22 p.
- U.S. Department of Agriculture. Hybrid Christmas tree... for the 1970s. *Agricultural Research*. 13(6): 8-9; 1964.
- U.S. Department of Agriculture, Forest Service. Silvicultural systems for the major forest types of the United States. Agriculture Handbook 445. Washington, DC: U.S. Department of Agriculture, Forest Service, Division of Timber Management Research; 1973. 124 p.
- Upton, Arthur T. Volume table for lodgepole pine. *Forestry Quarterly*. 12: 319-329; 1914.
- van den Driessche, R. J. *Pinus contorta* and its future prospect in this country. *Y coedwigwr [The Forester]*. 3(1): 5-7; 1956-1957.
- van Eerden, E.; Kinghorn, J. M., eds. Proceedings of the root form of planted trees symposium; 1978 May 16-19; Victoria, BC. Joint Report 8. Victoria, BC: British Columbia Ministry of Forests and Canadian Forestry Service; 1978. 157 p.
- Van Hooser, Dwane D.; Chojnacky, David C. Whole tree volume estimates for the Rocky Mountain States. Resource Bulletin INT-29. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 69 p.
- Wass, E. F. Ecology of shore pine stands infested with dwarf mistletoe on southeastern Vancouver Island. [Information Report] BC-X-142. Victoria, BC: Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre; 1976. 33 p.
- Weir, G. H.; Thurston, E. L. Scanning electron microscopic identification of fossil Pinaceae pollen to species by surface morphology. *Palynology*. 1: 157-165; 1977.
- Wellner, Charles A. The importance of lodgepole pine in the United States. In: Baumgartner, David M., ed. Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 1-9. (vol. 1).
- Wellner, Charles A.; Lowery, David P. Spiral grain—a cause of pole twisting. Research Paper INT-38. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1967. 17 p.
- Went, F. W. Rhizomorphs in soil not connected with fungal fruiting bodies. *American Journal of Botany*. 60(2): 103-110; 1973.
- Westman, Walter E. Edaphic climax pattern of the pygmy forest region of California. *Ecological Monographs*. 45(2): 109-135; 1975.
- Westman, Walter E. Patterns of nutrient flow in the pygmy forest region of northern California. *Vegetatio*. 36(1): 1-15; 1978.
- Westman, W. E.; Whittaker, R. H. The pygmy forest region of northern California: studies on biomass and primary productivity. *Journal of Ecology*. 63(2): 493-520; 1975.
- Wheeler, Nicholas C.; Critchfield, William B. The distribution and botanical characteristics of lodgepole pine: biographical and management implications. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. Lodgepole pine: the species and its management: symposium proceedings; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 1-13.
- Wheeler, Nicholas C.; Guries, Raymond P. Biogeography of lodgepole pine. *Canadian Journal of Botany*. 60(9): 1805-1814; 1982a.
- Wheeler, Nicholas C.; Guries, Raymond P. Population structure, genic diversity, and morphological variation in *Pinus contorta* Dougl. *Canadian Journal of Forest Research*. 12(3): 595-606; 1982b.
- Wikstrom, John H. Lodgepole pine—a lumber species. Research Paper 46. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1957. 15 p.
- Yeh, F. C.; Layton, C. The organization of genetic variability in central and marginal populations of lodgepole pine *Pinus contorta* spp. *latifolia*. *Canadian Journal of Genetics and Cytology*. 21(4): 487-503; 1979.
- Ying, Cheng C.; Illingworth, K.; Carlson, M. Geographic variations in lodgepole pine and its implications for tree improvement in British Columbia. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. Lodgepole pine: the species and its management: symposium proceedings; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 45-53.
- Ziegler, E. A., compiler. Forest tables—lodgepole pine. Circular 126. Washington, DC: U.S. Department of Agriculture, Forest Service; 1907. 24 p.

CHAPTER 2: MOISTURE CONTENT OF TREE COMPONENTS

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2-1 INTRODUCTION

Foliage, bark, and wood of living lodgepole pines commonly contain about 1 kg of water for each kilogram of dry biomass, but the ratio varies significantly among and within trees. For use as fuel, bark and foliage serve best if dry. Wood in use generally serves best if most of the water is removed because many of the desirable properties of wood are negatively correlated with moisture content. Some utilization processes require that water solutions be made to penetrate wood. For these reasons it is useful to know the location of water in trees and, while not within the scope of this chapter, the manner of its movement.

Moisture content is usually expressed as a percentage of oven-dry weight of wood, bark, or foliage, as follows.

Percentage moisture content =
[(weight with moisture - oven-dry weight)
/oven-dry weight] × 100

The oven-dry weight of wood, bark, and foliage is measured after drying it to constant weight in an oven held at 101 to 105 °C.

2-2 OBJECTIVE AND SCOPE

As previously noted, this characterization effort is confined to two varieties of lodgepole pine: *Pinus contorta* var. *latifolia* Engelm., and *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm., with emphasis on the former. The primary objective during tree collection was to obtain three replications of disease- and insect-free specimens of var. *latifolia* measuring 76, 152, and 228 mm in diameter at breast height (d.b.h.) at low, medium, and high elevations from nine equally spaced north latitudinal zones (40 to 60 degrees) across 10 degrees of longitude in such a way as to encompass the major range of this variety (fig. 1-1).

A secondary objective was to sample three replications of these same three diameter classes of var. *murrayana* at midelevation at four north latitudes (37.5, 40, 42.5, and 45 degrees) in California and Oregon at a single longitude per latitude (fig. 1-1).

The trees of both varieties were sampled in such a way that between-variety comparisons could be made for mid-elevation trees at latitudes 40, 42.5, and 45 degrees. The sampling plan does not permit computation of species-average values. The collection totaled 243 *latifolia* and 36 *murrayana* trees.

In this chapter variations in moisture contents of tree components are discussed. No attempt is made to construct equations for prediction of component moisture content. Instead, graphs are presented of data aggregated in various significant ways that permit readers to obtain moisture content information directly from the observed study data.

For *latifolia* some significant simple correlations are tabulated to aid subsequent students of the subject in developing predictive equations.

Explanations of statistical analyses procedures and a table of analyses of variance formats, with degrees of freedom indicated, are shown in table 1-2. In the results portion of this chapter standard deviations are noted in the text in parentheses following average values.

2-3 LITERATURE REVIEW

Yearly, Seasonal, and Daily Variation in Moisture Content

Because snow prevented access to upper elevations from early November to early June, tree collections were made during the months of June through October in 1983 and 1984. Interpretation of results reported here should be tempered with knowledge that some variation in tree component moisture content occurs with both year and season sampled. For example, Markstrom and Hann (1972) found that in five trees sampled each season near Fort Collins, CO, sapwood of 156- to 242-year-old *latifolia* had higher moisture content in 1967 than in 1968, and that moisture content was least in spring and most in fall and winter, as follows:

Year and season	Sapwood		Heartwood	
	Outer	Inner	Outer	Inner
	Percent of oven-dry weight			
1967				
Spring growing	138	138	35	43
Summer	145	144	42	48
Fall dormancy	161	147	39	47
Winter	173	164	43	68
1968				
Spring growing	127	131	36	47
Summer	150	150	42	55

The foregoing data are based on increment cores removed at 0.91 and 1.22 m above ground level.

Reid (1961) found that the moisture content of outer sapwood and inner bark of *latifolia* trees in British Columbia was about 10 percentage points greater at 4 a.m. than at 4 to 8 p.m.; noontime moisture content was intermediate. His data indicated an outer sapwood moisture content of about 150 percent, with inner sapwood having a much lower moisture content—about 50 percent; he observed that outer heartwood had about 25 percent moisture content, and innermost heartwood about 40 percent.

Live Branch Moisture Content

Dobie and McIntosh (1976) found that *latifolia* branches (wood plus bark) on 83 trees freshly harvested in late July and early August near Hinton, AB, had average moisture content of 74 percent of oven-dry weight.

Fahnestock (1960) found that whole branches (wood plus bark) from fresh *latifolia* logging slash in northern Idaho had a moisture content of 82 percent (nine samples); branchwood (one sample) averaged 96 percent.

Bark Moisture Content

Smith and Kozak (1971) found that *latifolia* trees in British Columbia had inner bark and outer bark moisture contents of 128 and 42 percent, respectively (oven-dry-weight basis). They provided no data on average moisture content for whole bark.

From other observations in British Columbia, Reid (1961) found that moisture content of inner bark of

latifolia stems was about 250 percent in May and June, but increased to 290 percent in July and August (ovendry-weight basis).

Stump-Root System Moisture Content

No data specific to lodgepole pine stump-root systems were found in the literature.

Foliage Moisture Content

In late July and early August 1975, Dobie and McIntosh (1976) sampled 83 *latifolia* trees shortly after they were harvested near Hinton, AB, and found that average foliage moisture content was 94 percent of ovendry weight.

Fahnestock (1960) found that foliage from fresh *latifolia* logging slash (one sample) in northern Idaho had a moisture content of 179 percent of ovendry weight.

Grouping data from a number of Rocky Mountain conifers (including *latifolia*), Brown (1978) observed that foliage moisture content was consistently greater than branchwood moisture content by about 24 percentage points. In dominant conifers, foliage moisture contents were highest in top portions of the crown and decreased downward through the crown; differences in foliage moisture content in crown sections of intermediates were much less than in dominants.

Stem Moisture Content

Dobie and McIntosh (1976) found that 83 *latifolia* stems (wood plus bark) sampled shortly after harvest in late July and early August near Hinton, AB, had average moisture content of 67 percent of ovendry weight.

In a study of *latifolia* trees in the Colorado Front Range, Dixon (1969) concluded that growth factors were unrelated to the moisture content of the wood in stems.

Similarly, from a study of stemwood of eighty-five 100-year-old *latifolia* trees growing near Hinton, AB, Johnstone (1970) found that tree-average stemwood moisture content was not closely correlated with other tree characteristics he measured; the best correlations were with dry needle weight per tree ($r = +0.37$), tree height ($r = +0.32$), and d.b.h. ($r = +0.30$). Moisture content of disks taken at various heights in the tree had correlations with other characteristics, as follows:

Characteristic	<i>r</i>
Height above ground	0.68
Age of disk	-.67
Average growth ring width	.43
Disk diameter inside bark	-.39
Disk specific gravity	-.38

From the 85 trees he examined a total of 713 disks; the moisture content of the 713 disks of stemwood averaged 85 percent of ovendry weight.

Johnstone found a curvilinear relationship between height in tree (feet) and percent moisture content of stemwood—ovendry-weight basis—as follows:

$$\text{Percent moisture content} = 0.697 + 0.000159H^2$$

For this equation, standard error of the estimate was 17.2 percentage points and r^2 was 0.49.

Average values for stemwood were as follows:

Position in tree	Percent moisture content (and standard deviation)
Within crown	99 (23)
At breast height	70 (12)
Tree average	79 (14)

Tree averages for stemwood in these 100-year-old trees ranged from a low of 45 percent to a high of 109 percent.

In British Columbia, Reid (1961) observed that the moisture content of *latifolia* sapwood is normally in the range from 85 to 165 percent of ovendry weight; he found heartwood to have about 30 percent moisture content. Substantial radial variation in the moisture contents of both sapwood and heartwood was observed (fig. 2-1).

Dead-Tree Moisture Content

This experiment was concerned only with insect- and disease-free live trees. Because of widespread mortality of lodgepole pine caused by insect attack, loss of moisture in standing dead trees is also of interest (fig. 2-1). Readers needing information on dead-tree moisture content will find useful the following references: Fahey (1980, 1981), Ince (1982), Lieu and others (1979), Lowery (1978), Lowery and Hearst (1978), Lowery and others (1977), Reid (1961), and U.S. Department of Agriculture, Forest Service (1948).

Additionally, the Pacific Northwest Forest and Range Experiment Station of the U.S. Department of Agriculture, Forest Service, has manuscripts in press on the subject—as does the Western Laboratory of FORINTEK CANADA CORP. in Vancouver, BC.

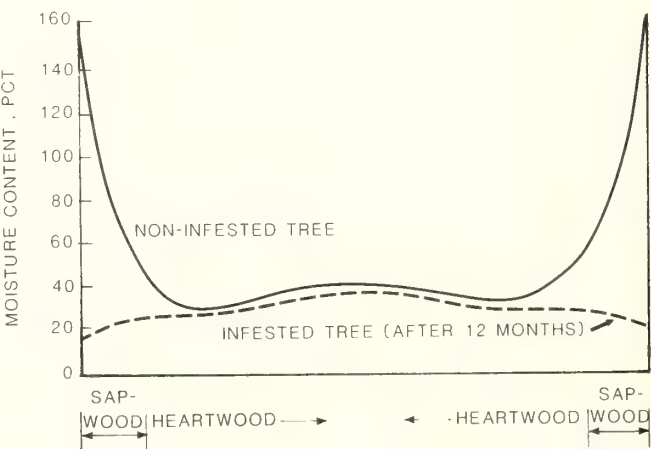


Figure 2-1—Radial variation of sapwood and heartwood moisture content (ovendry-weight basis) at 1.1-m level in a healthy *latifolia* stem, and in a stem 12 months after attack and infestation by the mountain pine beetle. (Drawing after Reid 1961.)

2-4 PROCEDURE

Procedural details of the study are given in chapter 1, and will not be repeated here except to note that the elevational zones of low, medium, and high are relative. Medium refers to an elevation that is medium for the variety at the latitude at which sampled; similarly, low and high refer to lower and upper elevational zones in which the variety occurs at the latitude sampled. *Latifolia* elevational zones were highest in the south (2,481, 2,711, and 3,144 m at 40 degrees) and progressively lower with each more northerly latitude (604, 739, and 879 m at 60 degrees). *Murrayana* was sampled at elevations in the range from 1,148 to 2,402 m.

Trees were uprooted (with central taproot intact and with lateral roots severed at a radius of 305 mm from tree pith) from level benches in natural unthinned stands within National or Provincial Forests. The sampling scheme resulted in selection of 76-, 152-, and 228-mm trees averaging 71, 91, and 107 years of age, respectively, for *latifolia*, and 67, 84, and 91 years for *murrayana*. Most of the small-diameter trees were suppressed, while the larger trees were the fast growers.

Table 2-1—Average moisture content of lodgepole pine tree components, with data from the 243 *latifolia* and the 36 *murrayana* trees pooled separately¹

Tree component	Variety	
	<i>Latifolia</i>	<i>Murrayana</i>
	Percent of oven-dry weight	
Complete tree with cones and foliage	96.6	108.6
Complete tree, wood only	95.9	108.0
Complete tree, bark only	103.3	113.7
Foliage	110.6	114.3
Cones (from first 305 mm of top 25 branches)	25.8	22.1
Dead branchwood	18.2	16.4
Live branches, wood plus bark	94.2	97.3
Live branchwood	88.6	92.7
Live branchbark	106.4	105.3
Stem, wood plus bark	99.4	111.6
Stemwood	98.9	111.2
Stembark	101.9	114.1
Sapwood	119.3	125.1
Heartwood	43.4	44.4
Stump-root system, wood plus bark	95.7	112.1
Stump-root system, wood only	94.9	110.8
Stump-root system, bark only	106.2	120.9
Stump, wood plus bark	88.8	99.8
Stumpwood	90.5	100.7
Stumpbark	77.3	92.1
Lateral roots, wood plus bark	106.3	125.1
Lateral roots, wood only	103.7	121.4
Lateral roots, bark only	120.7	140.2
Central root mass-taproot, wood plus bark	93.6	113.0
Central root mass-taproot, wood only	92.4	112.5
Central root mass-taproot, bark only	107.1	115.3

¹Because of the effects of d.b.h., latitude, and elevational zone, reference to appropriate figures and text discussion is required for interpretation of these data.

2-5 RESULTS—*LATIFOLIA*

Average moisture contents of tree components are summarized in table 2-1, but interpretation of these averages requires reference to the main effects and interactions attributable to d.b.h., latitude, and elevational zone—as discussed in the following paragraphs. Moisture contents throughout the paper are expressed as percentage of oven-dry weight.

Latitudinal sampling areas spanned 10 degrees of longitude (fig. 1-1), but no significant moisture-content variations attributable to longitudinal location along these 10-degree-wide sampling areas were detected.

In the following paragraphs summarizing results, only those main effects and interactions shown statistically significant (5-percent level) by analyses of variance are discussed, tabulated, and graphed.

Complete Tree With Cones and Foliage

Moisture contents of the 76-, 152-, and 228-mm diameter classes averaged—with standard deviations in parentheses following—98.5 (27.8), 96.7 (19.4), and 94.6 (18.3) percent of oven-dry weight. Low-elevation trees had less moisture content (94.7 percent) than those from medium- and high-elevation zones (97.5 percent), but moisture varied with latitude. Trees at 40 through 45 degrees latitude had from 105 to 120 percent moisture content, while those from 50 through 60 degrees of latitude had only 73 to 96 percent moisture (fig. 2-2).

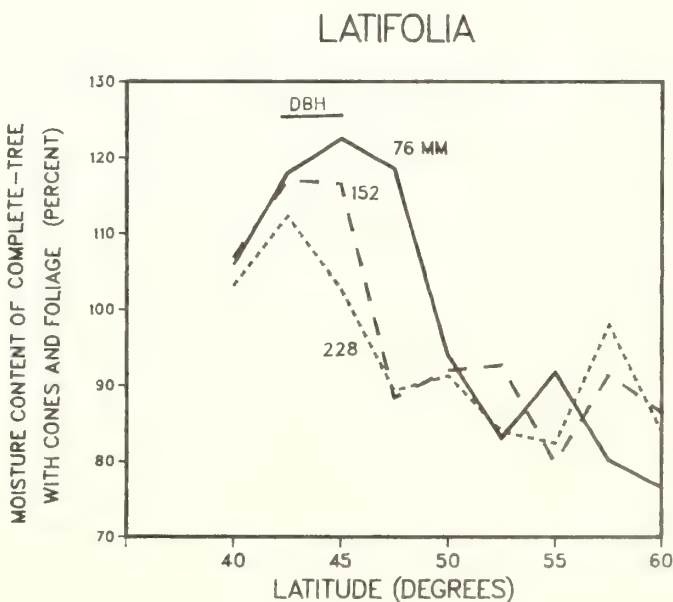


Figure 2-2—Moisture content of complete tree, with cones and foliage related to latitude for *latifolia* trees of three diameters.

Correlations between moisture content of complete tree with cones and foliage and the following measured properties are of interest:

Property	r
Moisture content of stem, wood plus bark, at 20 percent of tree height	0.870
Moisture content of stemwood at 152 mm stump height	.855
Moisture content of stump-root system, wood plus bark	.842
Heartwood volume percent of stemwood volume	-.759
Moisture content of live branches, wood plus bark	.733
Complete-tree bark specific gravity	-.587
Complete-tree wood specific gravity	-.572
Stemwood specific gravity	-.569
Sapwood specific gravity	-.537
Crown ratio	.521
Heartwood diameter at 152 mm stump height	-.432
Sapwood thickness at 152 mm stump height	.426

Complete Tree Without Cones or Foliage

Complete trees without cones or foliage, measuring 76, 152, and 228 mm in d.b.h., had average moisture contents of 98.5 (27.9), 96.7 (19.4), and 94.6 (18.3) percent. These moisture contents varied significantly with latitude, decreasing from 104 to 124 percent at 40 through 45 degrees, to 76 to 97 percent at 50 through 60 degrees (fig. 2-3).

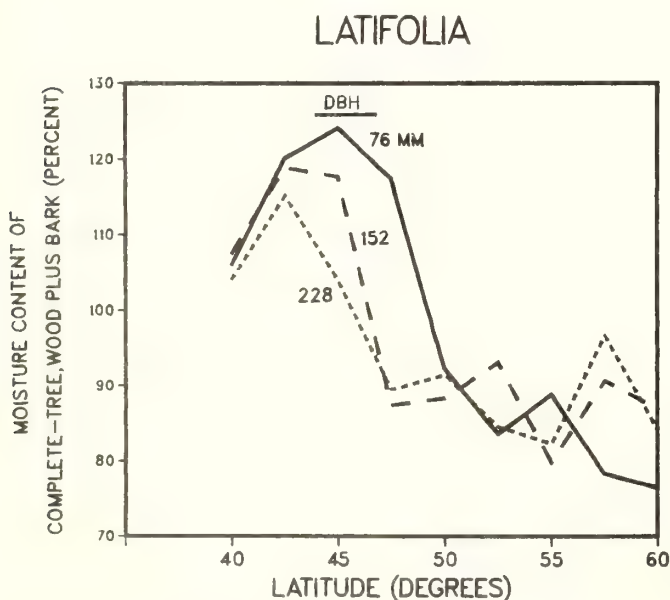


Figure 2-3—Moisture content of complete tree, wood plus bark—but without cones and foliage, related to latitude for *latifolia* trees of three diameters.

Correlations between moisture content of complete tree without cones or foliage and the following measured properties are of interest:

Property	r
Moisture content of stem, wood plus bark, at 20 percent of tree height	0.878
Moisture content of stemwood at 152 mm stump height	.859
Moisture content of stump-root system, wood plus bark	.841
Heartwood volume percent of stemwood volume	-.745
Moisture content of live branches, wood plus bark	.721
Complete-tree wood specific gravity	-.588
Stemwood specific gravity	-.586
Complete-tree bark specific gravity	-.577
Sapwood specific gravity	-.555
Crown ratio	.514
Sapwood thickness at 152 mm stump height	.440

Complete Tree, Wood Only

Complete-tree wood in trees of the three diameter classes did not vary greatly in average moisture content; with latitudinal and elevational data pooled, complete-tree wood of the 76-, 152-, and 228-mm trees averaged 96.0 (28.9), 96.7 (20.5), and 95.0 (18.9) percent moisture content. Variation with latitude was substantial, however; at latitudes 40 through 45 degrees wood moisture contents were in the range from 103 to 121 percent, while at latitudes 50 through 60 degrees complete-tree wood moisture contents were much lower—72 to 96 percent (fig. 2-4). At low elevations, treewood averaged 94.7 percent moisture

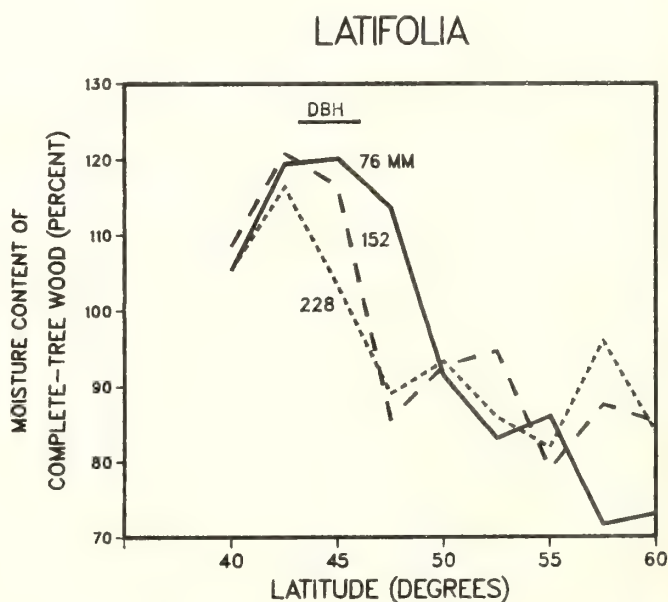


Figure 2-4—Moisture content of complete-tree wood related to latitude for *latifolia* trees of three diameters.

content, while at medium and high elevation the average was 97.5 percent—a difference not significant at the 5-percent level.

Correlations between moisture content of complete-tree wood and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stemwood at 20 percent of stem height	0.888
Moisture content of stemwood at 152 mm stump height	.870
Moisture content of stump-root system, wood only	.836
Moisture content of live branches, wood plus bark	.715
Heartwood volume percentage of stemwood volume	-.737
Complete-tree wood specific gravity	-.606
Stemwood specific gravity	-.604
Sapwood specific gravity	-.566
Complete-tree bark specific gravity	-.501
Crown ratio	.492
Sapwood thickness at 152 mm stump height	.483

Complete Tree, Bark Only

Moisture content of complete-tree bark (that of stem, stump-root, and branches) varied with latitude (fig. 2-5) and with elevational zone and diameter class, as follows:

Elevational zone	Average and standard deviation	
	---- Percent ----	
Low	98.3	(26.2)
Medium	106.5	(26.1)
High	104.9	(23.0)
D.b.h.	Average and standard deviation	
	---- Percent ----	
mm		
76	115.5	(28.0)
152	101.9	(22.2)
228	92.4	(19.7)
Average	103.3	(25.3)

Complete-tree bark moisture contents averaged highest at 45 degrees latitude (131 percent) and lowest at 52.5 degrees (81 percent) (fig. 2-5).

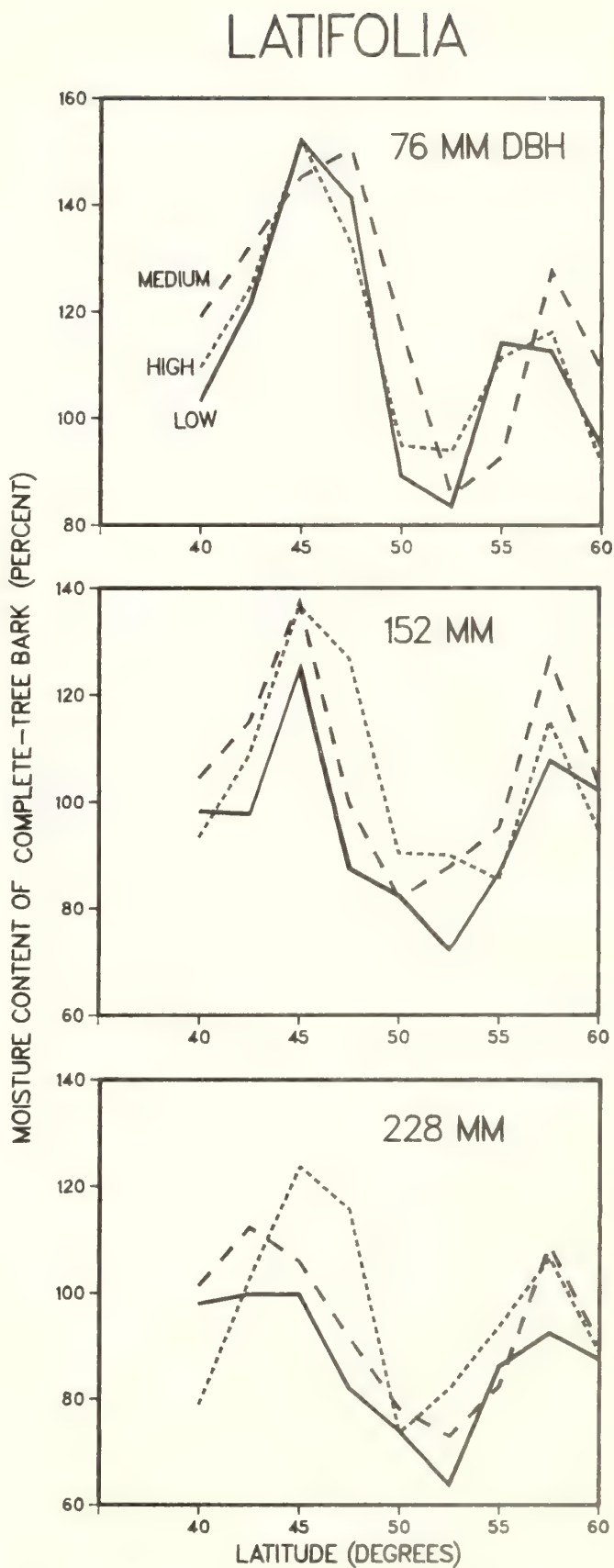
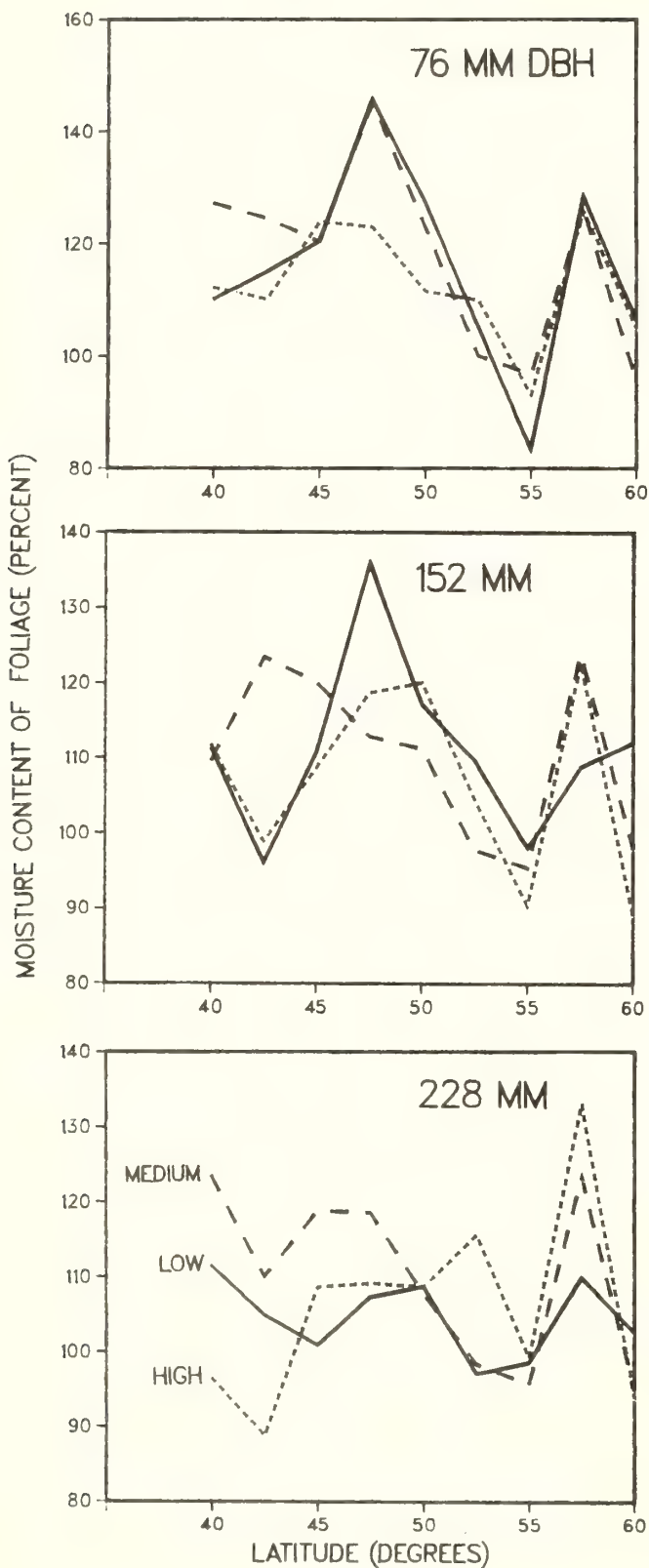


Figure 2-5—Moisture content of complete-tree bark related to elevational zone and latitude for *latifolia* trees of three diameters.

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Correlations between moisture content of complete-tree bark and the following measured properties are of interest:

Property	r
Moisture content of stembark	0.977
Complete-tree bark specific gravity	-.832
Moisture content of stembark at 20 percent of tree height	.815
Moisture content of stembark at 152 mm stump height	.759
Moisture content of live branchbark	.746
Moisture content of stump-root system, bark only	.720
Heartwood volume percentage of stemwood volume	-.564
Heartwood diameter at 152 mm stump height	-.541
Crown ratio	.471
Tree height	-.463

Foliage

Trees of small diameter had foliage with the highest moisture content, as follows:

D.b.h.	Average moisture content and standard deviation	
mm	----- Percent -----	
76	115.4	(17.5)
152	109.5	(14.9)
228	106.9	(15.1)
Average	110.6	(16.2)

Foliage from medium elevational zones averaged highest moisture content (average 112.7 percent), but elevational effects varied with latitude (fig. 2-6).

Correlations between foliage moisture content and measured properties were weak; those of interest follow:

Property	r
Moisture content of live branchbark	0.462
Moisture content of complete tree, bark only	.422
Specific gravity of complete-tree bark	-.355
Crown ratio	.310
Tree age	-.296
Tree height	-.294

Figure 2-6—Moisture content of foliage of *lati-folia* trees of three diameters related to elevational zone and latitude.

Cones

Cones from trees 76, 152, and 228 mm in d.b.h. had average moisture contents of 29.1 (27.8), 26.4 (20.0), and 23.7 (16.0) percent, but moisture content varied widely with latitude (fig. 2-7). With all data pooled, the average was 25.8 percent, with standard deviation of 20.4 percent.

Cone moisture content had little correlation with other measured tree properties; closest correlations are as follows:

Property	<i>r</i>
Moisture content of live branches, wood plus bark	0.263
Moisture content of dead branchwood	.240
Stump-root wood volume as percentage of treewood volume	.198

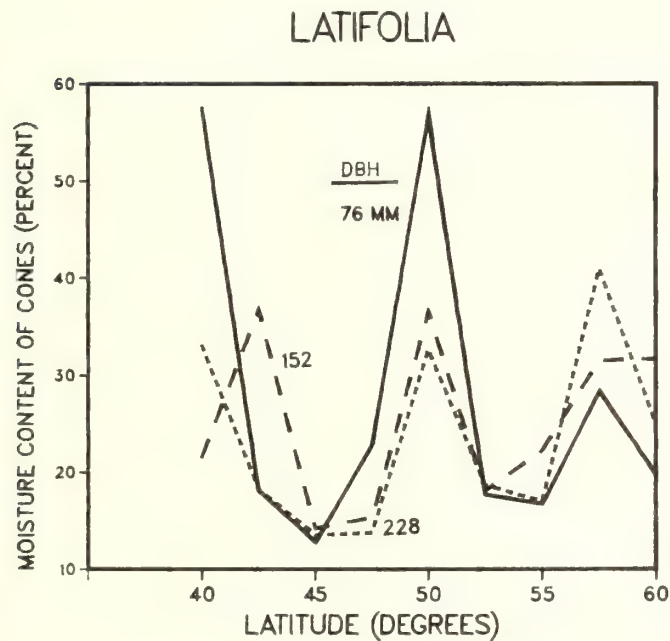


Figure 2-7—Moisture content of cones of *latifolia* trees of three diameter classes related to latitude.

Dead Branchwood

Moisture content of dead branchwood did not vary significantly with diameter but did vary with latitude (fig. 2-8); moisture content was lowest at 45 degrees latitude (14 percent) and highest at 57.5 degrees (28 percent). With all data pooled, dead branchwood averaged 18.2 percent moisture content, with standard deviation of 9.9 percent.

As with cones, moisture content of dead branchwood was poorly correlated with other measured tree properties; closest correlations were as follows:

Property	<i>r</i>
Moisture content of foliage	0.256
Moisture content of cones	.240
Dead branchwood percent of complete-tree wood volume	.212

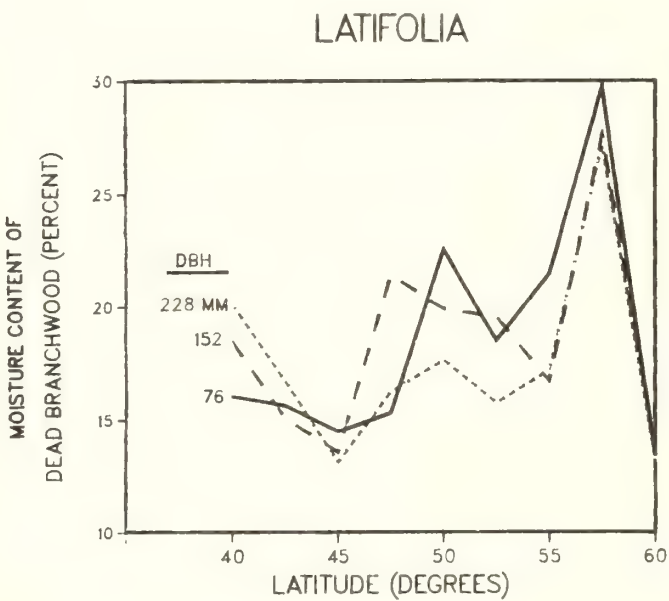


Figure 2-8—Moisture content of dead branchwood related to latitude for *latifolia* trees of three diameters.

Live Branches, Wood Plus Bark

The moisture content of foliage-free live branches (wood plus bark) did not vary significantly with d.b.h. or with elevational zone but did vary with latitude (fig. 2-9); moisture contents were highest at latitude 42.5 degrees (106 percent) and lowest at 60 degrees (83 percent). With all data pooled, live branches (wood plus bark) had average moisture content of 94.2 percent, with standard deviation of 15.9 percent.

Correlations between moisture content of live branches (wood plus bark) and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of complete tree with cones and foliage	0.733
Moisture content of branch-free stem, wood plus bark	.695
Moisture content of stem, wood plus bark, at 50 percent of tree height	.664
Moisture content of stem, wood plus bark, at 152 mm stump height	.618
Moisture content of stump-root system, wood plus bark	.600
Heartwood volume as percentage of stem-wood volume	-.542
Specific gravity of live branchwood	-.532
Specific gravity of complete-tree wood	-.481
Specific gravity of stemwood	-.467
Specific gravity of complete-tree bark	-.457
Specific gravity of sapwood	-.447
Sapwood thickness at 152 mm stump height	.409

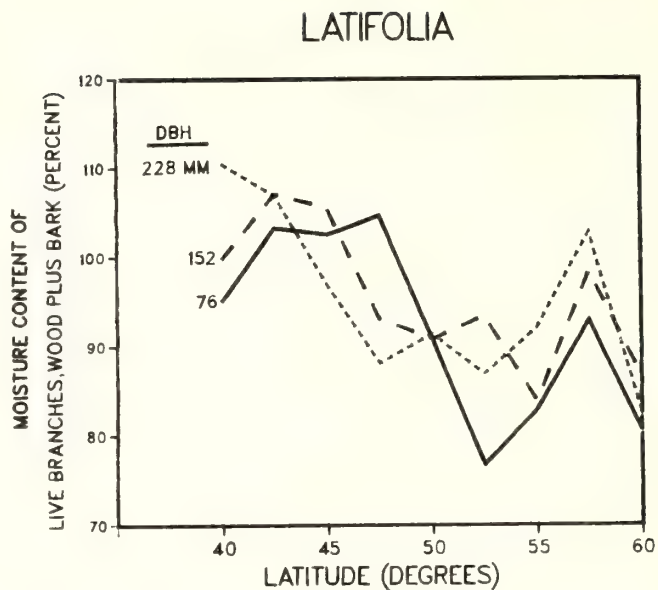


Figure 2-9—Moisture content of live branches, wood plus bark, related to latitude for *latifolia* trees of three diameters.

Live Branchwood

Branchwood moisture content in trees of 76-, 152-, and 228-mm d.b.h. averaged 84.2 (17.9), 90.4 (17.1), and 91.1 (16.4) percent. In low-, medium-, and high-elevation zones branchwood averaged 90.5, 88.9, and 86.3 percent moisture content, but varied with latitude (fig. 2-10). Branchwood moisture content had highest moisture content at 42.5 degrees (104 percent) and lowest at 60 degrees (77 percent).

Correlations between moisture content of live branchwood and the following properties are of interest:

Property	<i>r</i>
Specific gravity of live branchwood	-.629
Moisture content of complete-tree wood	.599
Moisture content of sapwood	.583
Moisture content of stemwood	.575
Moisture content of stemwood at 70 percent of tree height	.572
Moisture content of stemwood at 152 mm stump height	.524
Moisture content of lateral roots, wood only	.439
Heartwood volume as percentage of stemwood volume	-.416
Specific gravity of complete-tree wood	-.410
Specific gravity of stemwood	-.393

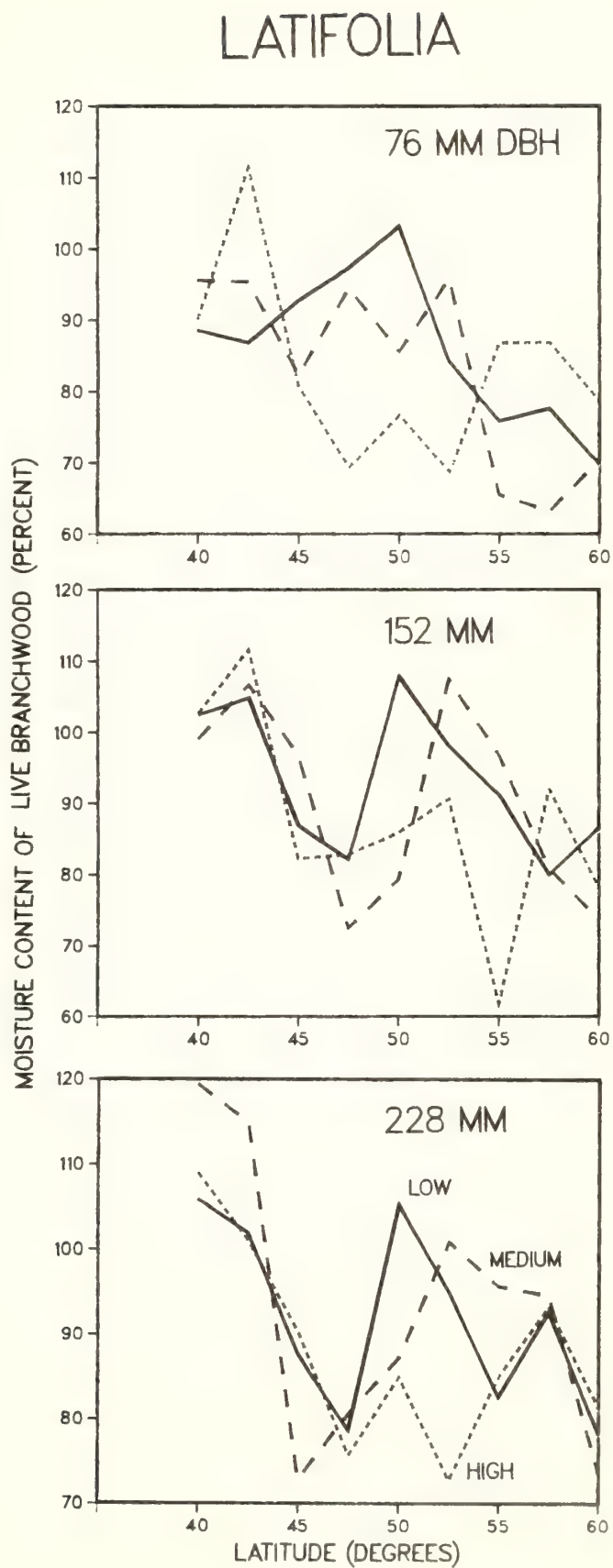


Figure 2-10—Moisture content of live branchwood related to latitude and to elevational zone for *latifolia* trees of three diameters.

Live Branchbark

The moisture content of the bark of live branches averaged 106.4 percent, with standard deviation of 25.8 percent, and varied significantly only with latitude (fig. 2-11). Branchbark moisture content averaged highest at 45 degrees (132 percent) and lowest at 52.5 degrees (79 percent).

Correlations between moisture content of live branchbark and the following measured properties are of interest:

Property	<i>r</i>
Specific gravity of complete-tree bark	-0.679
Moisture content of stembark at 50 percent of tree height	.639
Moisture content of stembark	.634
Moisture content of complete tree with cones and foliage	.573
Moisture content of stump-root system, bark only	.510
Moisture content of stemwood	.499
Crown ratio	.425
Heartwood volume percent of stemwood volume	-.401

Stem, Wood Plus Bark—Tree Average

The moisture content of branch-free stems, wood plus bark, averaged 99.4 percent, with standard deviation of 24.5 percent. Trees 76, 152, and 228 mm in d.b.h. averaged 100.9 (30.6), 100.1 (21.9), and 97.2 (19.9) percent moisture content, but varied with latitude (fig. 2-12). Stems had highest moisture content at 42.5 degrees (122 percent) and lowest at 60 degrees (85 percent).

Correlations between tree-average moisture content of stem (wood plus bark) and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of complete tree with cones and foliage	0.983
Moisture content of stem (wood plus bark) at 20 percent of tree height	.885
Moisture content of sapwood	.866
Moisture content of stem (wood plus bark) at 152 mm stump height	.849
Moisture content of stump-root system, wood plus bark	.802
Heartwood volume as percentage of stemwood volume	-.733
Moisture content of live branches, wood plus bark	.695
Specific gravity of stemwood	-.579
Specific gravity of complete-tree wood	-.574
Specific gravity of complete-tree bark	-.559
Sapwood specific gravity	-.551
Crown ratio	.507

LATIFOLIA

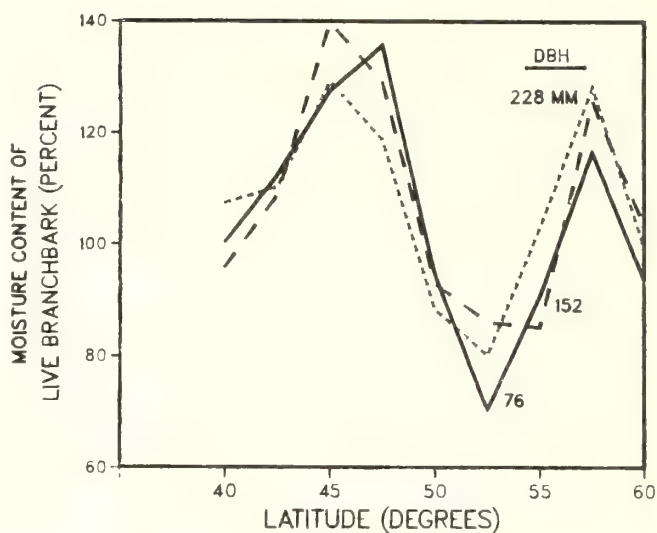


Figure 2-11—Moisture content of live branchbark related to latitude for *latifolia* trees of three diameters.

LATIFOLIA

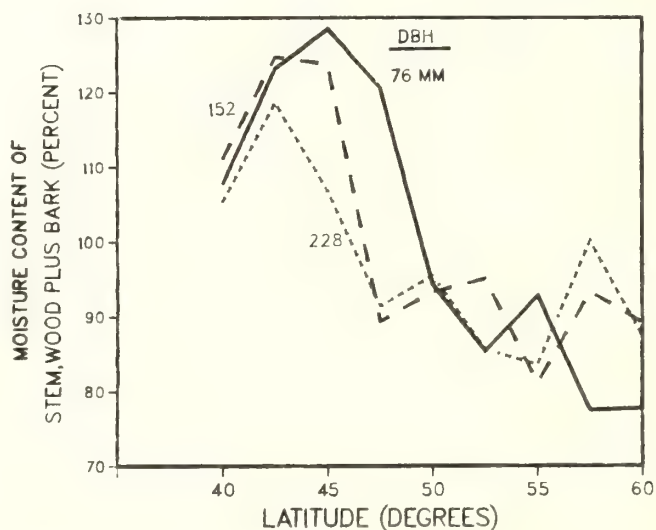


Figure 2-12—Moisture content of branch-free stem, wood plus bark, related to latitude for *latifolia* trees of three diameters.

Stem, Wood Plus Bark—Variation With Height

Moisture content of stems, wood plus bark, was positively correlated with height in tree, with minimum of 89 percent at stump-top level, and increasing to 137 percent at 90 percent of tree height; at the apical tip tissues averaged 187 percent moisture content (fig. 2-13). Latitudinal effects on moisture content of the branch-free stem (wood plus bark) were similar at all heights in the trees (fig. 2-14).

Of the tree heights for which correlations were analyzed (0, 20, 50, and 70 percent of tree height from stump top to apical tip), the moisture content at 20 percent height provided the closest correlations for most moisture contents of interest, as follows (except for live branch moisture content—which was best correlated with 50 percent height where $r = 0.664$; and moisture content of wood and bark of the stump-root system—which were best correlated with 0 percent height where $r = 0.752$):

Property	<i>r</i>
Moisture content of entire branch-free stem, wood plus bark	0.885
Moisture content of complete tree without cones or foliage	.878
Moisture content of complete tree with cones and foliage	.870
Moisture content of sapwood	.783

Moisture contents of stem (wood plus bark) at 0, 20, and 50 percent heights were a little more closely correlated with heartwood volume as a percentage of stemwood volume (-0.779 , -0.774 , -0.787) than the moisture content at 70 percent height ($r = -0.734$).

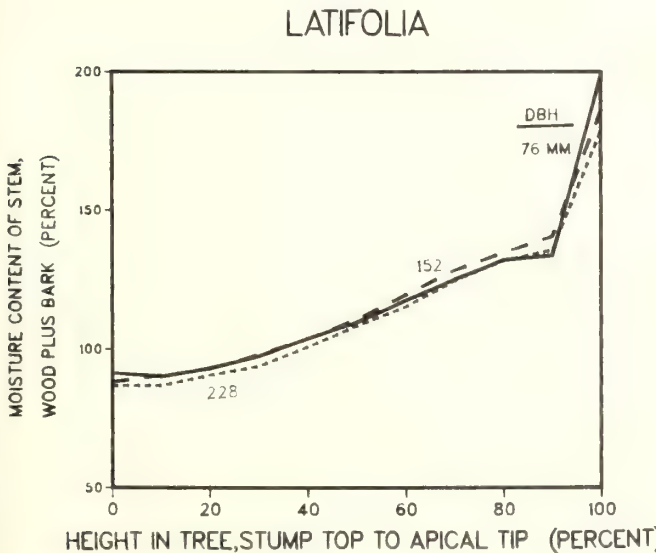


Figure 2-13—Moisture content of branch-free stem, wood plus bark, related to height in tree for *latifolia* trees of three diameters.

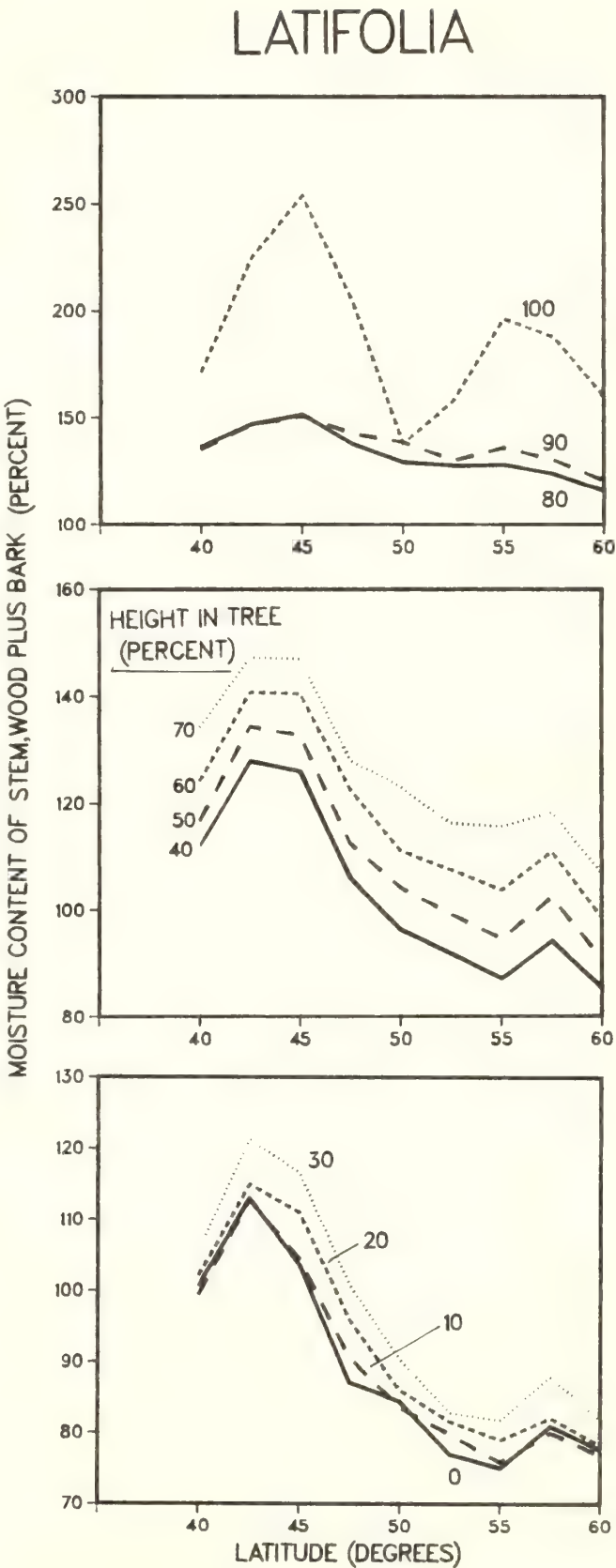


Figure 2-14—Moisture content of branch-free stem, wood plus bark, related to height in tree and to latitude, with data from the three diameter classes of *latifolia* trees pooled.

Stemwood—Tree Average

Stemwood of the trees had average moisture content of 98.9 percent, with standard deviation of 25.4 percent. By d.b.h. the averages did not differ appreciably but did differ with latitude (fig. 2-15). In southern latitudes the 76-mm trees had high moisture content but in northern latitudes had lowest moisture content. With diameter data pooled, stemwood moisture content was highest at 42.5 degrees (124 percent) and lowest at 60 degrees (83 percent).

Correlations between tree-average moisture content of stemwood and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of complete tree without cones or foliage	0.992
Moisture content of complete tree with cones and foliage	.972
Moisture content of stemwood at 20 percent of tree height	.891
Moisture content of sapwood	.886
Moisture content of stemwood at 152 mm stump height	.859
Moisture content of wood of stump-root system	.794
Heartwood volume as percentage of stemwood volume	-.722
Moisture content of live branches, wood plus bark	.695
Specific gravity of stemwood	-.600
Specific gravity of complete-tree wood	-.595
Specific gravity of sapwood	-.566
Specific gravity of complete-tree bark	-.498
Crown ratio	.492
Sapwood thickness at 152 mm stump height	.473

Stemwood—Variation With Height

Stemwood moisture content was about 90 percent at stump height and at 10 percent of tree height; above these heights moisture content increased to 130 percent in the upper stem (fig. 2-16). The decrease in stemwood moisture content in northerly latitudes was evident at all heights in the stem (fig. 2-17).

LATIFOLIA

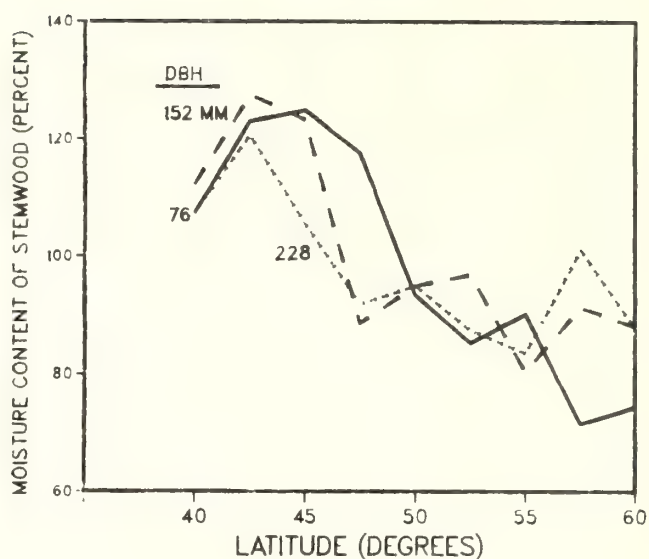


Figure 2-15—Moisture content of stemwood related to latitude for *latifolia* trees of three diameters.

LATIFOLIA

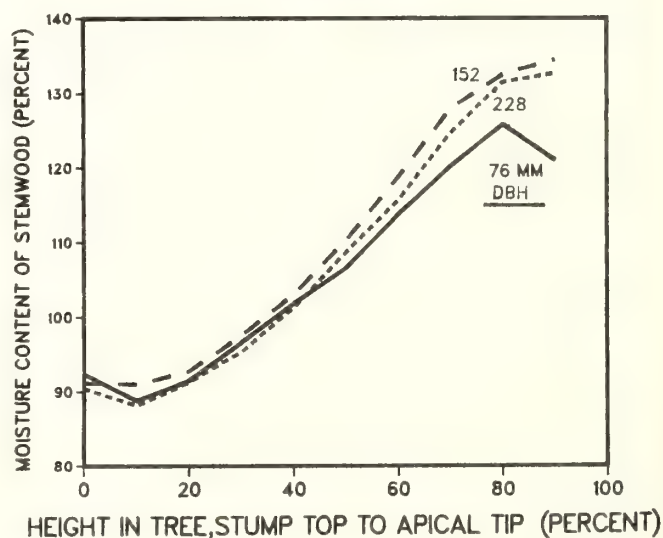


Figure 2-16—Moisture content of stemwood related to height in tree for *latifolia* trees of three diameters.

The moisture content of wood of the stump-root system was best correlated with stemwood moisture content at 152 mm stump height ($r = 0.756$); that of live branchwood was best correlated with stemwood moisture content at 70 percent height ($r = 0.572$).

Stemwood moisture content at 20 percent of tree height was more closely correlated with moisture contents of entire stemwood ($r = 0.891$), complete-tree wood ($r = 0.888$), and sapwood ($r = 0.801$) than stemwood moisture contents at 0, 50, or 70 percent of tree height.

Stemwood moisture content at 152 mm stump height was more closely correlated with stemwood specific gravity ($r = -0.643$) and heartwood volume percent of stemwood volume ($r = -0.771$) than stemwood moisture contents at 20, 50, or 70 percent of tree height.

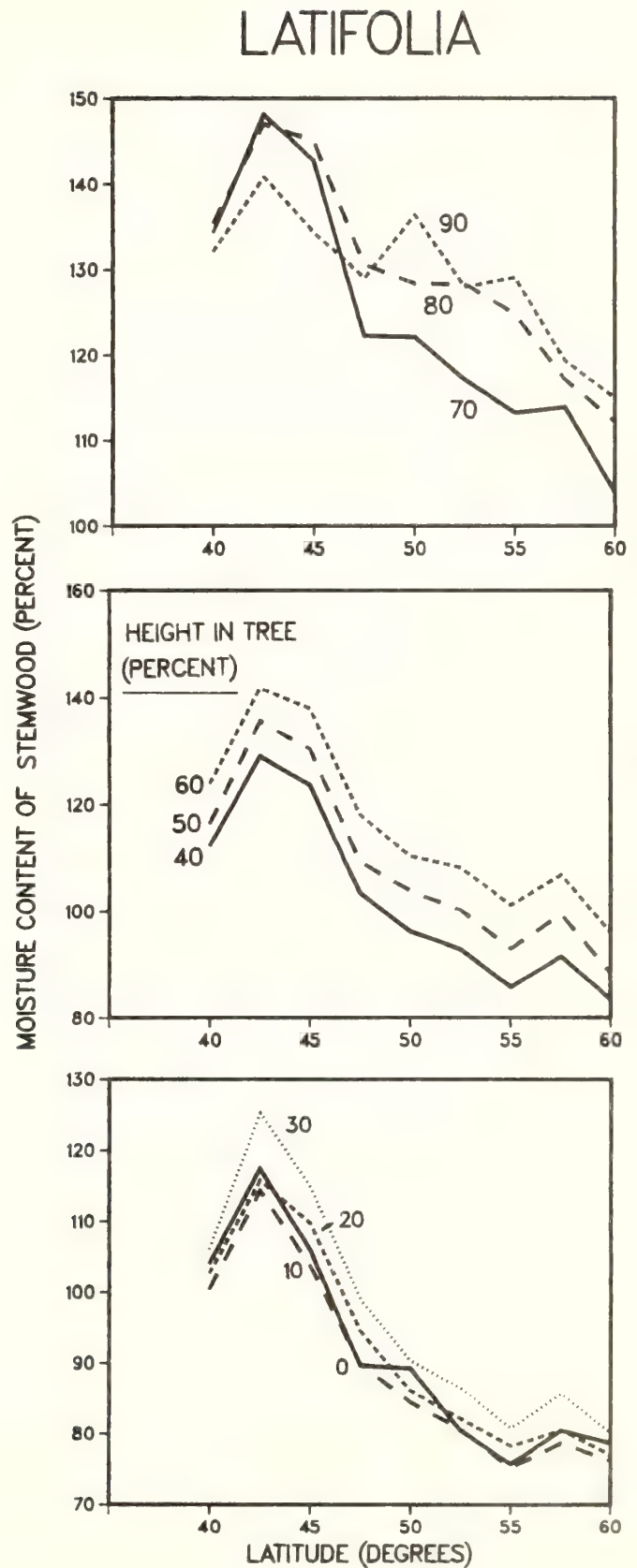


Figure 2-17—Moisture content of stemwood related to height in tree and to latitude, with data from the three diameter classes of *latifolia* trees pooled.

Stembark—Tree Average

Stembark had slightly higher moisture content than stemwood, averaging 101.9 percent, with standard deviation of 28.6 percent. Stembark moisture content was inversely correlated with d.b.h., averaging 118.8 (31.2), 100.9 (23.6), and 86.2 (20.1) percent for d.b.h. classes of 76, 152, and 228 mm.

Stembark moisture content also varied significantly with elevational zone, as follows:

Elevational zone	Average moisture content and standard deviation	
	----- Percent -----	
Low	97.1	(29.9)
Medium	105.1	(30.2)
High	103.1	(25.2)

Stembark moisture content also varied with latitude (fig. 2-18); it was highest at 45 degrees (131 percent) and lowest at 52.5 degrees (80 percent).

Correlations between tree-average moisture content of stembark and the following measured properties are of interest:

Property	r
Moisture content of complete-tree bark	0.977
Moisture content of stembark at 20 percent of tree height	.826
Specific gravity of complete-tree bark	-.799
Moisture content of stembark at 152 mm stump height	.779
Moisture content of bark of stump-root system	.641
Moisture content of live branchbark	.634
Heartwood diameter at 152 mm stump height	-.603
Heartwood volume as percentage of stemwood volume	-.562
Tree height	-.516
Stem weight (wood plus bark), ovendry	-.493
Complete-tree bark as percentage of complete-tree volume	.489
Weight of stump-root system, ovendry	-.471
D.b.h.	-.469
Crown ratio	.429

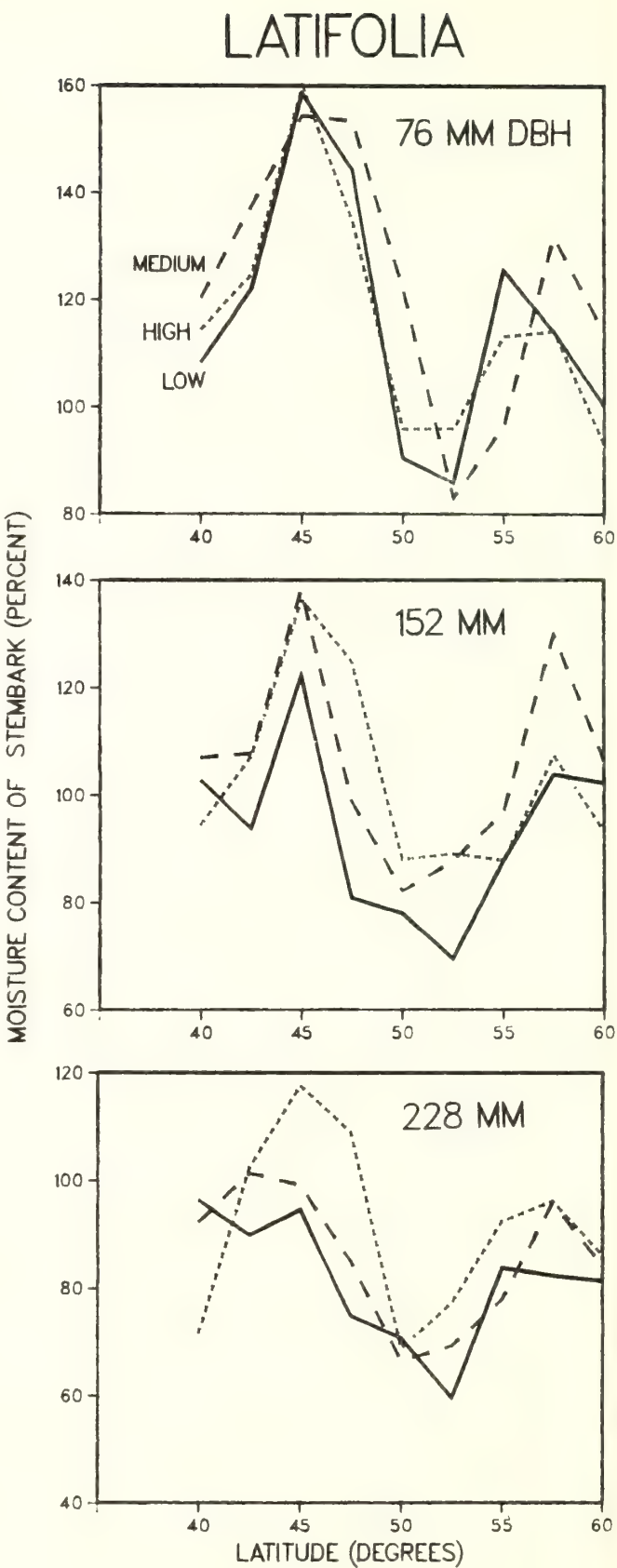


Figure 2-18—Moisture content of stembark related to latitude and to elevational zone for *latifolia* trees of three diameters.

Stembark—Variation With Height

Stembark moisture content was lowest at stump height (72 percent average) and increased more or less linearly with height in tree to 165 percent average in the upper stem (fig. 2-19). Latitudinal trends were similar for all heights in the stem (fig. 2-20).

Of the heights analyzed (0, 20, 50, and 70 percent), moisture content of stembark at 20 percent of tree height was most closely correlated with the following properties of interest:

Property	<i>r</i>
Moisture content of stembark, tree average	0.826
Specific gravity of complete-tree bark	-.821
Heartwood volume as percentage of stem-wood volume	-.615
Moisture content of complete tree with cones and foliage	.589

Moisture content of live branchbark was best correlated with stembark moisture content at 50 percent of tree height ($r = 0.639$). Moisture content of the stump-root system was best correlated with moisture content of the stembark at 152 mm stump height ($r = 0.567$).

LATIFOLIA

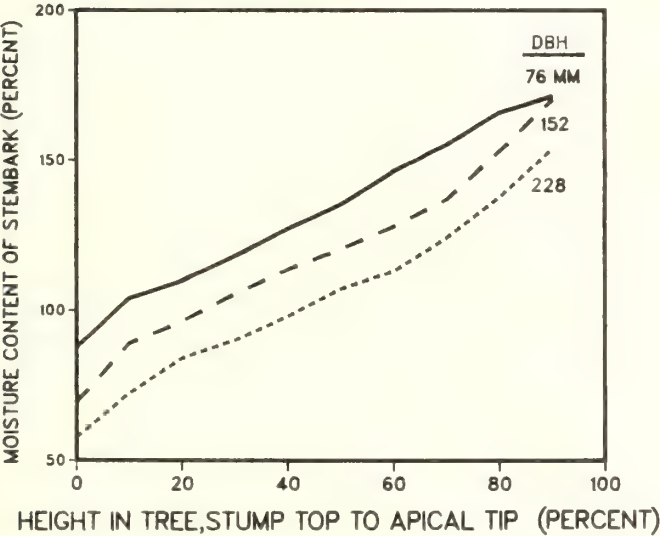


Figure 2-19—Moisture content of stembark related to height in tree for *latifolia* trees of three diameters.

LATIFOLIA

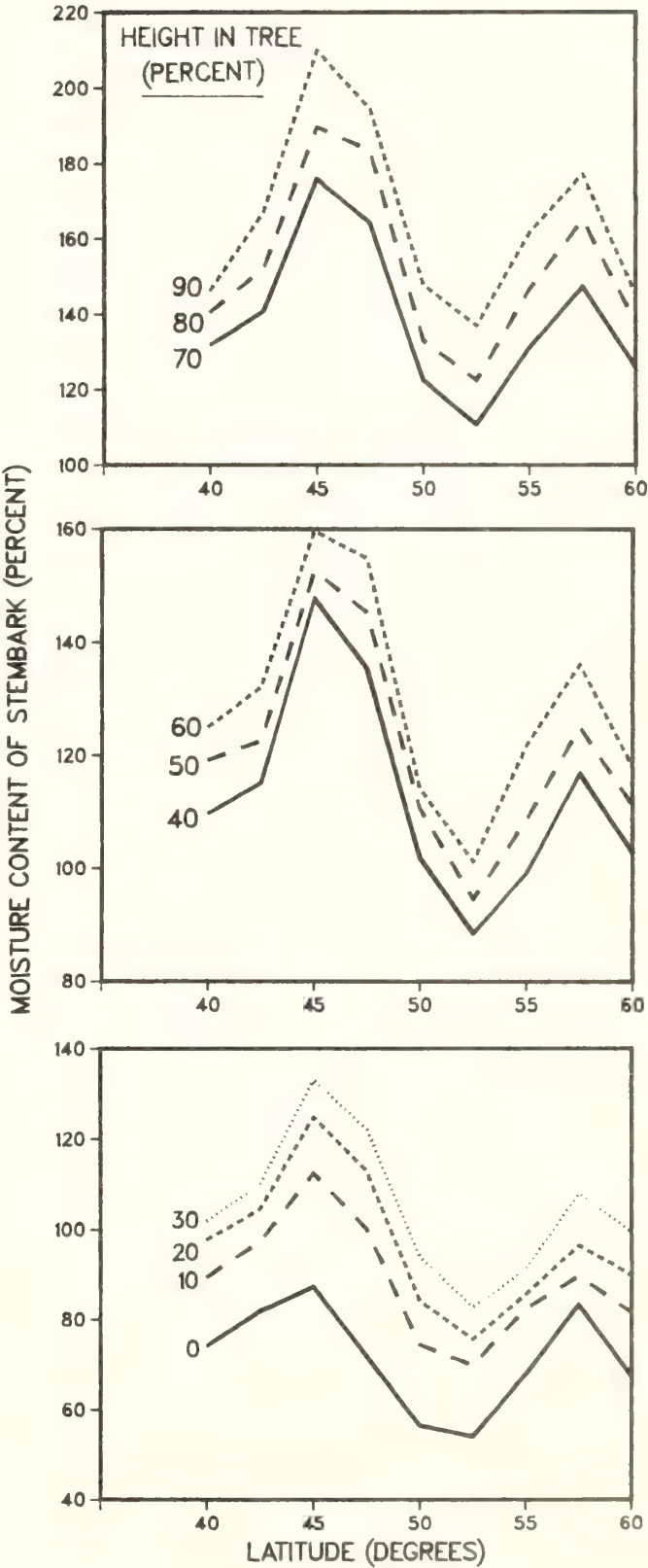


Figure 2-20—Moisture content of stembark related to height in tree and to latitude, with data from the three diameter classes of *latifolia* trees pooled.

Sapwood

Sapwood moisture content averaged 119.3 percent, with standard deviation of 23.1 percent. The smallest trees had lowest sapwood moisture content, as follows:

D.b.h. mm	Moisture content and standard deviation	
	Percent	
76	110.1	(28.5)
152	121.7	(18.6)
228	126.1	(17.7)

This relationship changed at 45 degrees latitude where trees of all three diameters had sapwood with the same moisture content, and at 47.5 degrees where sapwood moisture content was higher in 76-mm trees than in 228-mm trees (fig. 2-21). Sapwood moisture content averaged highest at latitude 42.5 degrees (139 percent) and lowest at 55 degrees (108 percent).

Correlations between sapwood moisture content and the following measured properties are of interest:

Property	r
Moisture content of complete-tree wood	0.872
Moisture content of complete tree with cones and foliage	.827
Moisture content of stemwood at 20 percent of tree height	.801
Moisture content of stemwood at 152 mm stump height	.754
Specific gravity of stemwood	-.689
Specific gravity of complete-tree wood	-.679
Specific gravity of sapwood	-.678
Moisture content of live branches, wood plus bark	.643
Moisture content of stump-root system, wood plus bark	.601
Sapwood thickness at 152 mm stump height	.522
Heartwood volume as percentage of stemwood volume	-.428
Specific gravity of live branchwood	-.422
Live branchwood as percentage of complete-tree wood volume	.403

LATIFOLIA

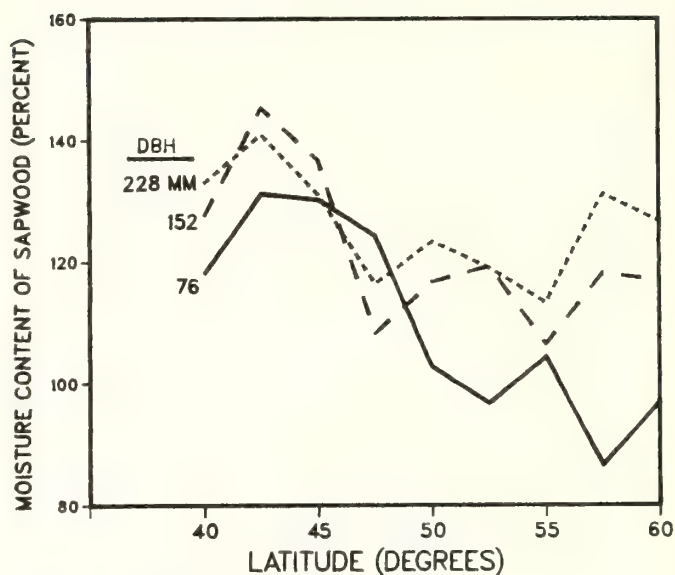


Figure 2-21—Moisture content of sapwood related to latitude for *latifolia* trees of three diameters.

Heartwood

Heartwood moisture content was much less than that of sapwood; it averaged 43.4 percent, with standard deviation of 5.7 percent. Heartwood moisture content was inversely correlated with d.b.h., averaging 47.2 (6.9), 41.9 (3.8), and 40.9 (3.8) percent in trees 76, 152, and 228 mm in d.b.h.

In contrast to sapwood, the smallest trees had highest heartwood moisture content at all latitudes, and variation with latitude was less pronounced in heartwood than in sapwood—especially in larger trees (fig. 2-22).

Heartwood moisture content was poorly correlated with moisture contents of other tree portions; the closest correlations were with stem moisture contents at 152 mm stump height and at 70 percent of tree height (r for both = 0.341) and with moisture content of entire stembark (r = 0.396). Other correlations of interest are as follows:

Property	r
Tree height	-0.537
Complete-tree bark as percentage of gross complete-tree volume	.501
Stembark as percentage of gross stem volume	.479
Sapwood weight, ovendry	-.461
Stump-root wood volume as percentage of treewood volume	.452
D.b.h.	-.449
Stem weight, wood plus bark, ovendry	-.447
Specific gravity of complete-tree bark	-.441
Weight of stump-root system, ovendry	-.440
Heartwood diameter at 152 mm stump height	-.434

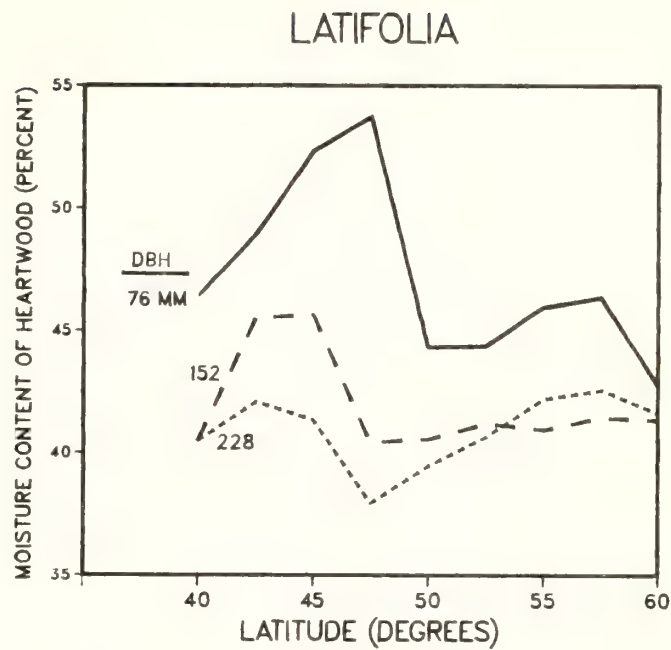


Figure 2-22—Moisture content of heartwood related to latitude for *latifolia* trees of three diameters.

Stump-Root System, Wood Plus Bark

Wood plus bark of the stump-root systems had average moisture content of 95.7 percent, with standard deviation of 23.1 percent. Trees 76, 152, and 228 mm in d.b.h. had moisture contents of 101.3 (26.1), 93.0 (19.1), and 92.7 (22.7) percent.

Stump-root moisture contents in trees of all three diameters decreased significantly in northern latitudes (fig. 2-23); maximums were at 42.5 degrees (120 percent) and minimums at 60 degrees (80 percent).

Correlations between moisture content of the gross stump-root system and the following measured properties are of interest:

Property	r
Moisture content of complete tree with cones and foliage	0.842
Moisture content of complete tree without cones or foliage	.841
Moisture content of branch-free stem, wood plus bark	.802
Moisture content of stemwood	.786
Heartwood volume as percentage of stem-wood volume	-.668
Moisture content of live branches, wood plus bark	.600
Specific gravity of wood of stump-root system	-.586
Specific gravity of complete-tree wood	-.538
Specific gravity of stemwood	-.507
Crown ratio	.466
Specific gravity of sapwood	-.461

Stump-Root System, Wood Only

Wood of the stump-root systems averaged 94.9 percent moisture content, with standard deviation of 23.7 percent. Wood of trees 76-, 152-, and 228-mm d.b.h. had moisture contents of 99.5 (27.7), 92.0 (20.1), and 93.1 (22.1) percent, but these percentages varied with latitude (fig. 2-24). Wood of the stump-root systems averaged highest moisture content at 42.5 degrees latitude (133 percent) and lowest at 60 degrees (90 percent).

Correlations between moisture content of the wood of the stump-root system and the following measured properties are of interest:

Property	r
Moisture content of complete tree with cones and foliage	0.842
Moisture content of complete tree without cones or foliage	.841
Moisture content of branch-free stem, wood plus bark	.802
Heartwood volume as percentage of stem-wood volume	-.680
Moisture content of sapwood	.620
Specific gravity of wood of stump-root system	-.613
Moisture content of live branches, wood plus bark	.604
Specific gravity of complete-tree wood	-.564
Specific gravity of stemwood	-.531

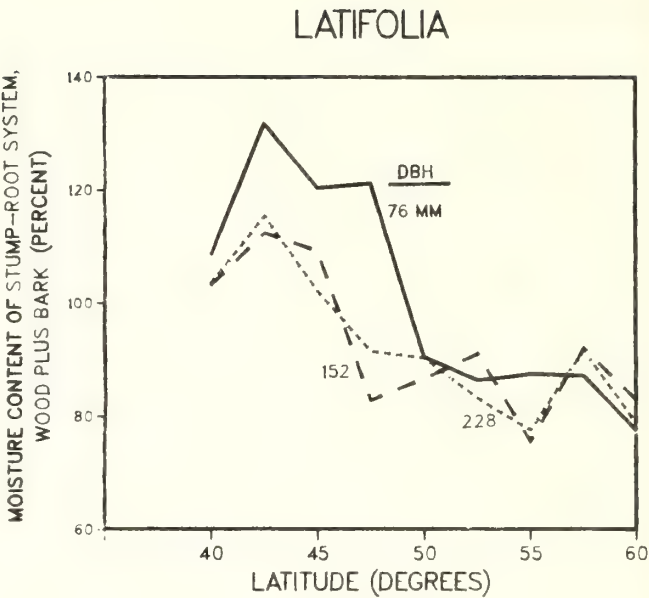


Figure 2-23—Moisture content of stump-root system, wood plus bark, related to latitude for latifolia trees of three diameters.

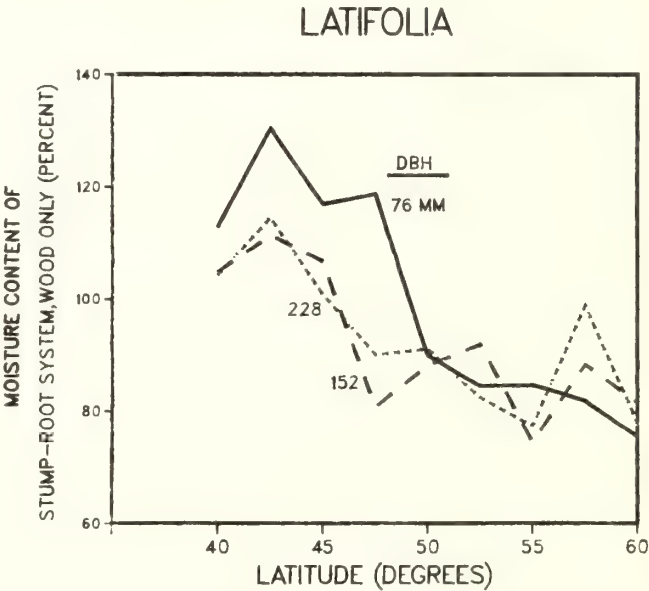


Figure 2-24—Moisture content of wood of the stump-root system related to latitude for latifolia trees of three diameters.

Stump-Root System, Bark Only

Bark of the stump-root systems had average moisture content of 106.2 percent, with standard deviation of 26.5 percent. Bark moisture content was inversely correlated with d.b.h., averaging 116.1 (29.0), 102.0 (24.5), and 100.4 (23.2) for trees 76, 152, and 228 mm in diameter.

Bark moisture content varied with elevational zone, as follows:

Elevational zone	Average moisture content and standard deviation	
	----- Percent -----	
Low	96.9	(24.3)
Medium	108.4	(27.7)
High	113.3	(25.0)

Bark of the stump-root systems had highest moisture content at 42.5 degrees latitude (133 percent) and lowest at 50 degrees (89 percent) (fig. 2-25).

Correlations between moisture content of the bark of the stump-root system and the following measured properties are of interest:

Property	r
Moisture content of complete-tree bark	0.720
Moisture content of stembark	.641
Specific gravity of complete-tree bark	-.588
Moisture content of complete tree with cones and foliage	.575
Moisture content of complete tree without cones or foliage	.571
Moisture content of stembark at 152 mm stump height	.567
Moisture content of branch-free stem, wood plus bark	.533
Heartwood volume as percentage of stem-wood volume	.436

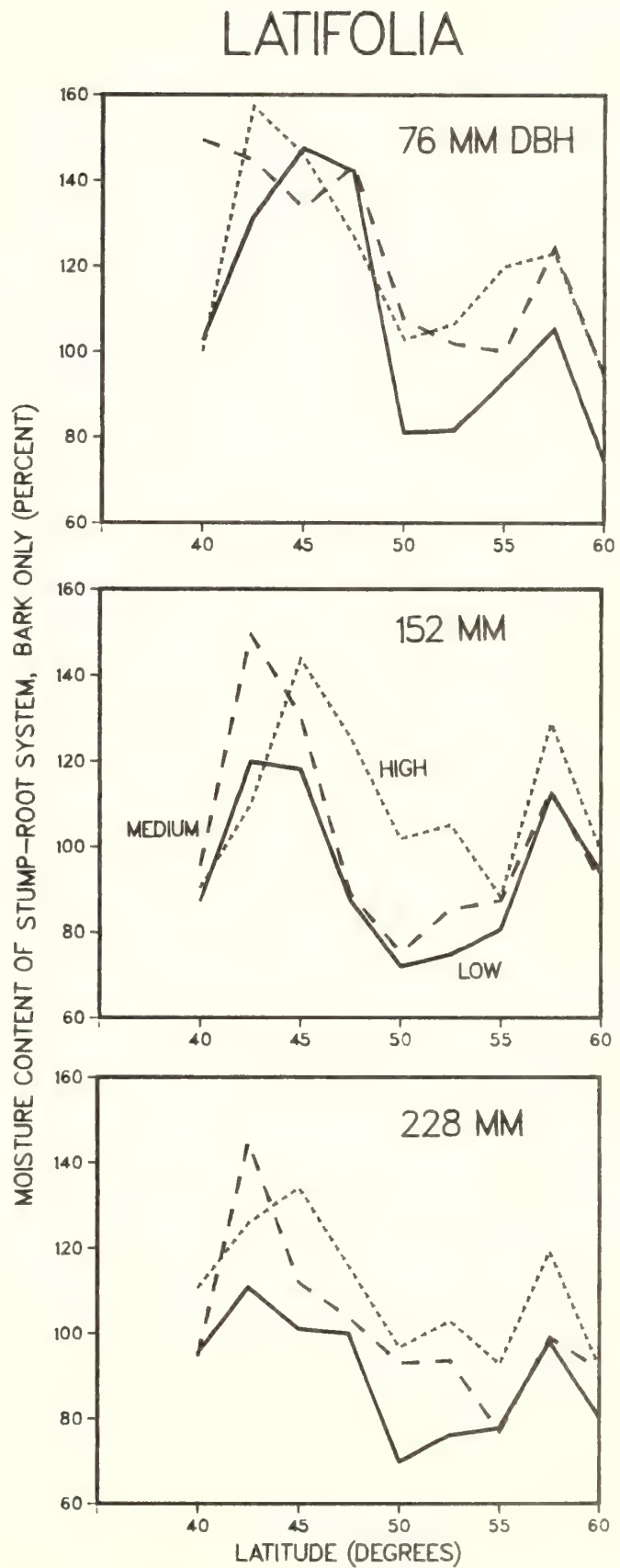


Figure 2-25—Moisture content of bark of the stump-root system related to latitude and to elevational zone for latifolia trees of three diameters.

Stump, Wood Plus Bark

Wood plus bark in the stump from ground level to 152-mm-high stump top had average moisture content of 88.8 percent, with standard deviation of 25.3 percent. In trees of 76-, 152-, and 228-mm d.b.h., stumpwood plus bark had moisture contents of 94.2 (28.7), 85.8 (23.4), and 86.3 (22.7) percent, but varied significantly with latitude (fig. 2-26). Stumpwood plus bark moisture contents averaged highest at 42.5 degrees latitude (117 percent) and least at 55 degrees (72 percent).

Correlations between moisture content of the stump (wood plus bark) and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stem, wood plus bark, at 152 mm stump height	0.848
Moisture content of complete tree without cones or foliage	.757
Moisture content of complete tree with cones and foliage	.756
Moisture content of branch-free stem, wood plus bark	.728
Heartwood volume as percentage of stem-wood volume	-.728
Specific gravity of complete-tree bark	-.552
Specific gravity of complete-tree wood	-.507
Specific gravity of wood of stump-root system	-.497
Specific gravity of stemwood	-.490

Stumpwood

Stumpwood had average moisture content of 90.5 percent, with standard deviation of 27.3 percent, and had little correlation with d.b.h. In trees from low-elevation zones, stumpwood had higher moisture content (93.4 percent) than in those from medium-elevation zones (87.9 percent) or high zones (90.3 percent), but the relationship varied with latitude. Stumpwood had highest moisture content at 42.5 degrees latitude (119 percent) and lowest at 55 degrees (73 percent) (fig. 2-27).

Correlations between stumpwood moisture content and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stemwood at 152 mm stump height	0.834
Moisture content of complete-tree wood	.741
Moisture content of complete tree with cones and foliage	.737
Heartwood volume as percentage of stem-wood volume	-.716
Moisture content of stemwood	.713
Moisture content of sapwood	.569
Moisture content of live branches, wood plus bark	.513
Specific gravity of complete-tree wood	-.502
Specific gravity of stemwood	-.487
Specific gravity of complete-tree bark	-.477
Specific gravity of wood of stump-root system	-.476

LATIFOLIA

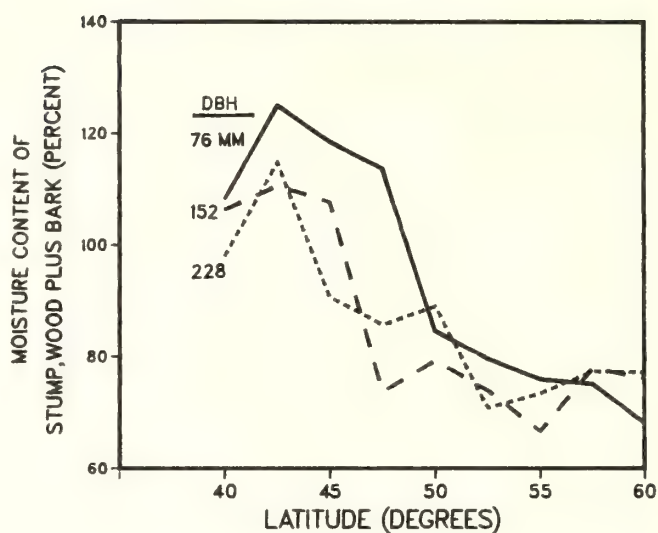


Figure 2-26—Moisture content of stump from groundline to stump top, wood plus bark, related to latitude for *latifolia* trees of three diameters.

LATIFOLIA

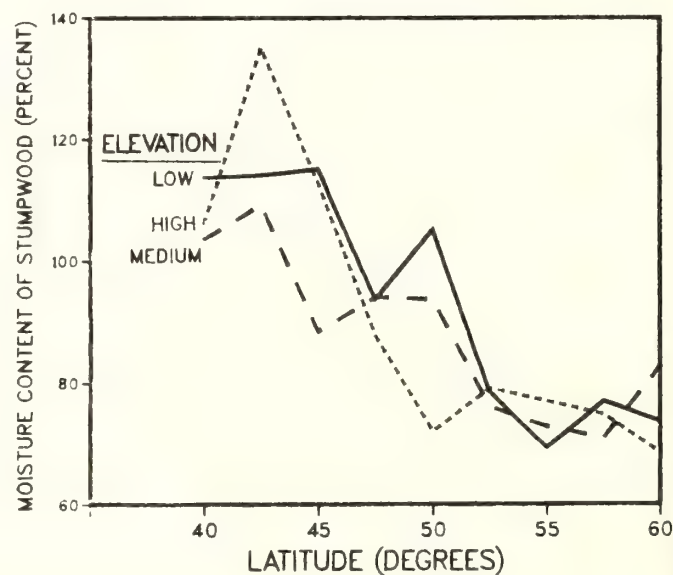


Figure 2-27—Moisture content of stumpwood (groundline to stump top) related to latitude for *latifolia* trees in three elevational zones.

Stumpbark

Moisture content of stumpbark averaged 77.3 percent, with standard deviation of 27.6 percent; it was inversely correlated with d.b.h., averaging 93.6 (30.4), 73.6 (24.1), and 64.8 (18.9) percent for trees 76, 152, and 228 mm in diameter. It was positively correlated with elevational zone, as follows:

Elevational zone	Average moisture content and standard deviation	
	----- Percent -----	
Low	72.8	(26.4)
Medium	74.1	(25.5)
High	85.1	(29.3)

Stumpbark moisture content varied with latitude (fig. 2-28); it was highest at 42.5 degrees (98 percent) and lowest at 50 degrees (56 percent).

Correlations between stumpbark moisture content and the following measured properties are of interest:

Property	r
Moisture content of stump-root system, bark only	0.764
Specific gravity of complete-tree bark	-.606
Tree height	-.502
Heartwood diameter at 152 mm stump height	-.500
Complete-tree bark percentage of gross complete-tree volume	.478
Stem weight, wood plus bark, ovendry	-.451
Heartwood volume as percentage of stem-wood volume	-.435
Moisture content of branchbark	.432
D.b.h.	-.425

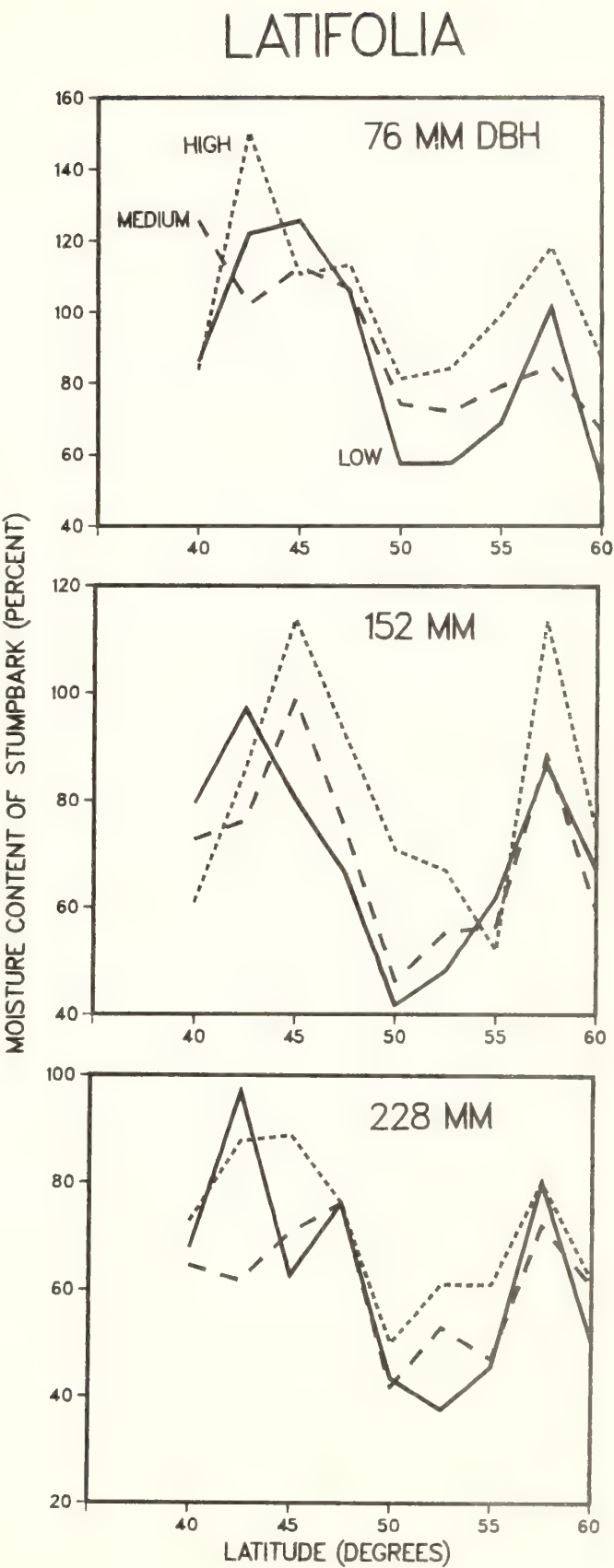


Figure 2-28—Moisture content of stumpbark (groundline to stump top) related to latitude and to elevational zone for *latifolia* trees of three diameters.

Lateral Roots, Wood Plus Bark

Wood plus bark of lateral roots from root collar to 152 mm radius from tree pith averaged 106.3 percent moisture content, with standard deviation of 25.5 percentage points. Trees 76, 152, and 228 mm in d.b.h. had lateral root moisture contents of 113.0 (29.2), 104.0 (22.5), and 101.7 (23.3) percent, but these averages were significantly related to both latitudinal and elevational zones (fig. 2-29). Moisture contents averaged highest at 42.5 degrees latitude (131 percent) and least at 55 degrees (84 percent).

Correlations between the moisture content of lateral roots (wood plus bark) and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stem, wood plus bark, at 152 mm stump height	0.827
Moisture content of complete tree with cones and foliage	.767
Moisture content of complete tree without cones or foliage	.761
Heartwood volume as percentage of stem-wood volume	-.749
Moisture content of stem, wood plus bark	.729
Specific gravity of complete-tree bark	-.596
Specific gravity of wood of stump-root system	-.577
Moisture content of live branches, wood plus bark	.572
Specific gravity of complete-tree wood	-.570
Specific gravity of stemwood	-.557
Specific gravity of sapwood	-.515
Crown ratio	.514
Heartwood diameter at 152 mm stump height	-.501

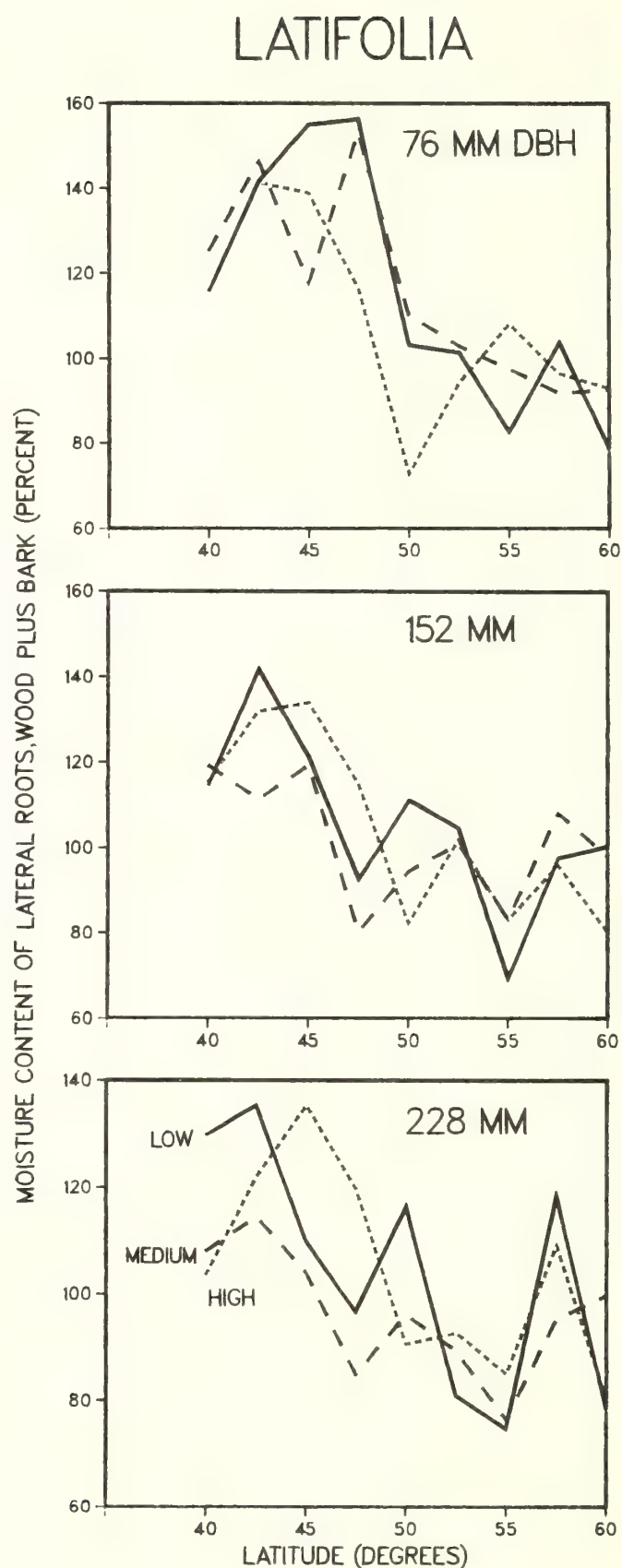


Figure 2-29—Moisture content of lateral roots from root collar to 305 mm radius from tree pith, wood plus bark, related to latitude and elevational zone for *latifolia* trees of three diameters.

Lateral Roots, Wood Only

Moisture content of lateral root wood did not vary significantly with tree diameter; with diameter data pooled, moisture content averaged 103.7 percent, with standard deviation of 26.5 percentage points. Lateral root wood moisture content was, however, significantly related to both latitude and elevational zone (fig. 2-30), with trees from low-elevation zones having slightly higher moisture content (107 percent) than those from the other two zones (102 percent). Moisture contents averaged highest at 42.5 degrees latitude (130 percent) and lowest at 55 degrees (81 percent).

Correlation between the moisture content of lateral root wood and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stemwood at 152 mm stump height	0.822
Moisture content of complete tree with cones and foliage	.766
Moisture content of complete tree without cones or foliage	.762
Heartwood volume as percentage of stemwood volume	-.751
Moisture content of branch-free stem, wood plus bark	.732
Specific gravity of complete-tree wood	-.596
Specific gravity of wood of stump-root system	-.590
Moisture content of live branches, wood plus bark	.586
Specific gravity of stemwood	-.583
Moisture content of sapwood	.571
Specific gravity of complete-tree bark	-.539
Specific gravity of sapwood	-.535
Crown ratio	.500

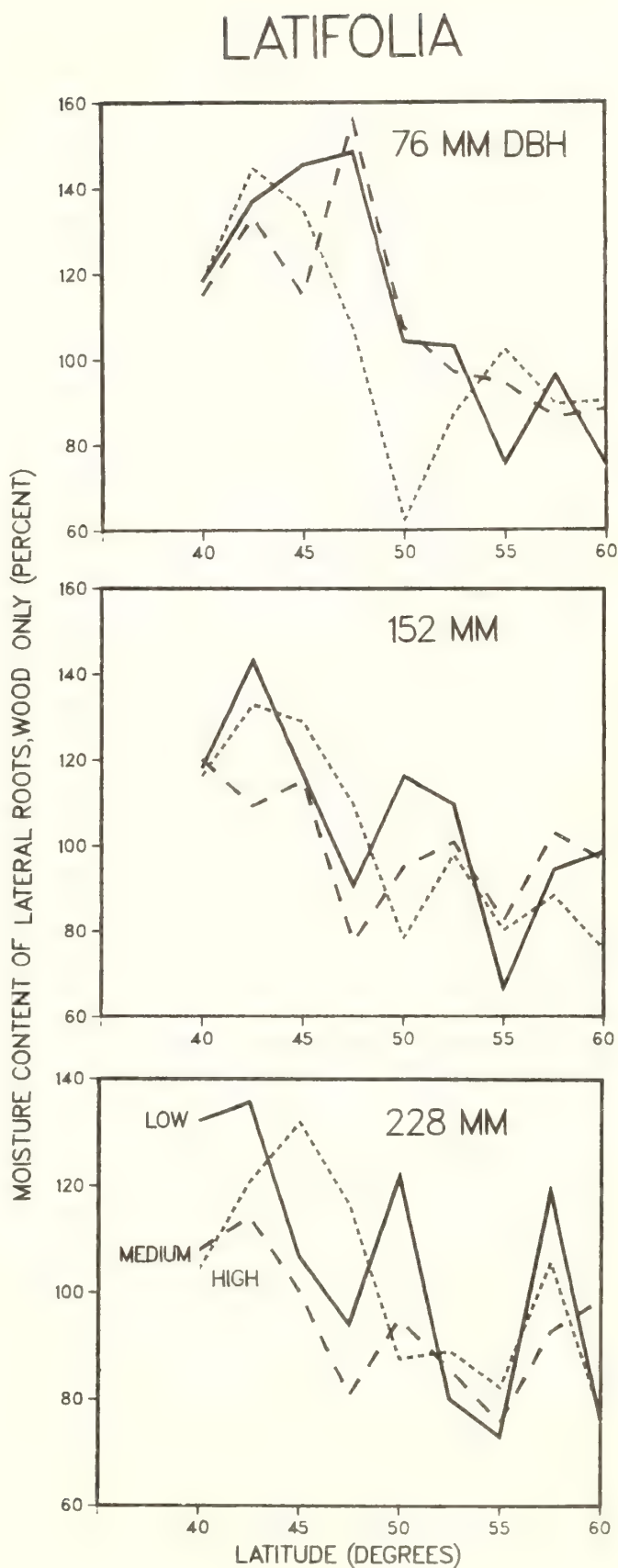


Figure 2-30—Moisture content of wood in lateral roots, from root collar to 305 mm radius from tree pith, related to latitude and elevational zone for *latifolia* trees of three diameters.

Lateral Roots, Bark Only

Moisture content of bark of the lateral roots averaged 120.7 percent, with standard deviation of 31.7 percentage points. Trees 76, 152, and 228 mm in d.b.h. had bark moisture contents of 130.7 (37.5), 118.0 (29.0), and 113.3 (25.3) percent. High-elevation trees had moister bark than low—particularly those 152 and 228 mm in d.b.h. (fig. 2-31). Bark of the lateral roots had highest moisture content at 45 degrees latitude (153 percent) and lowest moisture content at 55 degrees (101 percent).

Correlations between the moisture content of lateral rootbark and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of complete-tree bark	0.625
Specific gravity of complete-tree bark	-.583
Moisture content of stembark at 20 percent of tree height	.570
Moisture content of live branches, wood plus bark	.555
Moisture content of complete tree with cones and foliage	.512
Heartwood volume as percentage of stem-wood volume	-.439

LATIFOLIA

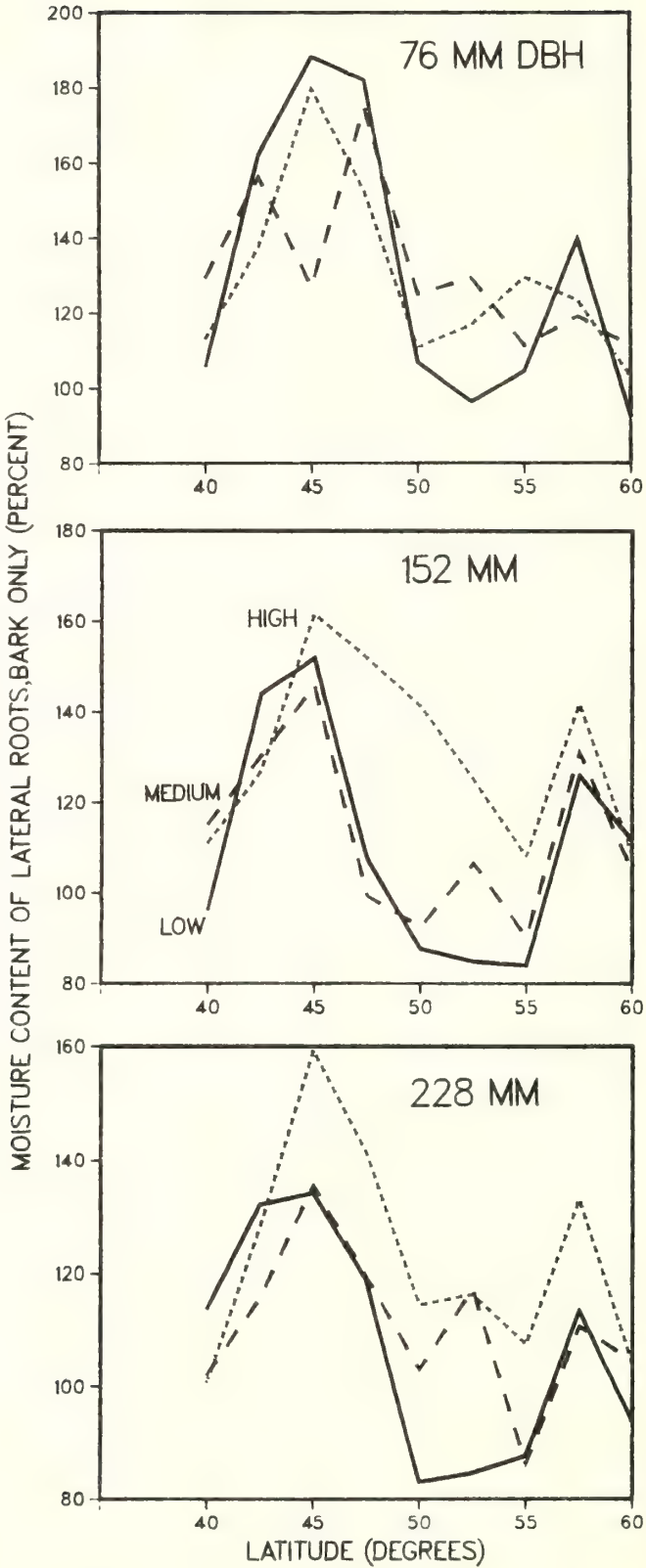


Figure 2-31—Moisture content of bark in lateral roots, from root collar to 305 mm radius from tree pith, related to latitude and to elevational zone for *latifolia* trees of three diameters.

Central Root Mass-Taproot, Wood Plus Bark

Wood plus bark of the central root mass-taproot shorn of laterals and stump had average moisture content of 93.6 percent, with standard deviation of 25.0 percentage points. In southerly latitudes, 76-mm trees had more moisture content than the two larger diameter classes (fig. 2-32). Moisture content of wood plus bark averaged highest at 42.5 degrees latitude (115.7 percent) and lowest at 60 degrees (73 percent).

Correlations between the moisture content of the wood plus bark of the central root mass-taproot and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stem, wood plus bark, at 152 mm stump height	0.711
Moisture content of complete tree with cones and foliage	.694
Moisture content of complete tree without cones or foliage	.688
Specific gravity of wood of the stump-root system	-.684
Heartwood volume as percentage of stem-wood volume	-.677
Moisture content of branch-free stem, wood plus bark	.645
Moisture content of live branches, wood plus bark	.539
Specific gravity of complete-tree bark	-.527
Specific gravity of complete-tree wood	-.513

Central Root Mass-Taproot, Wood Only

Wood of the central root mass-taproot had average moisture content of 92.4 percent, with standard deviation of 25.7 percentage points. Moisture content varied significantly with diameter, averaging 97.9 (28.9), 88.8 (23.6), and 90.4 (23.6) percent for trees 76, 152, and 228 mm in d.b.h.

Wood of the central root mass-taproot had highest moisture content at 42.5 degrees latitude (116 percent) and lowest at 60 degrees (73 percent) (fig. 2-33).

Correlations between the moisture content of the wood of the central root mass-taproot and the following measured properties are of interest:

Property	<i>r</i>
Moisture content of stemwood at 152 mm stump height	0.705
Moisture content of complete tree with cones and foliage	.703
Moisture content of complete-tree wood	.693
Specific gravity of the wood of the stump-root system	-.686
Heartwood volume as percentage of stem-wood volume	-.683
Moisture content of stemwood	.651
Moisture content of live branches, wood plus bark	.550
Specific gravity of complete-tree wood	-.546
Specific gravity of complete-tree bark	-.506
Specific gravity of stemwood	-.501

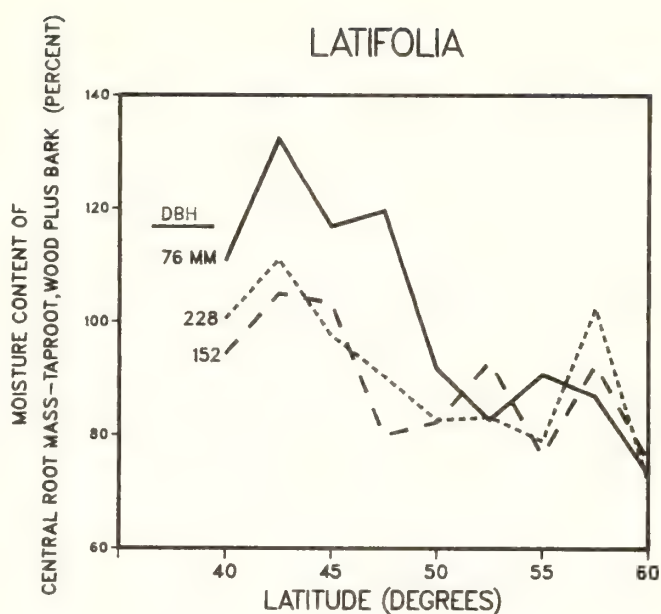


Figure 2-32—Moisture content of central root mass and taproot shorn of stump and laterals, wood plus bark, related to latitude for *latifolia* trees of three diameters.

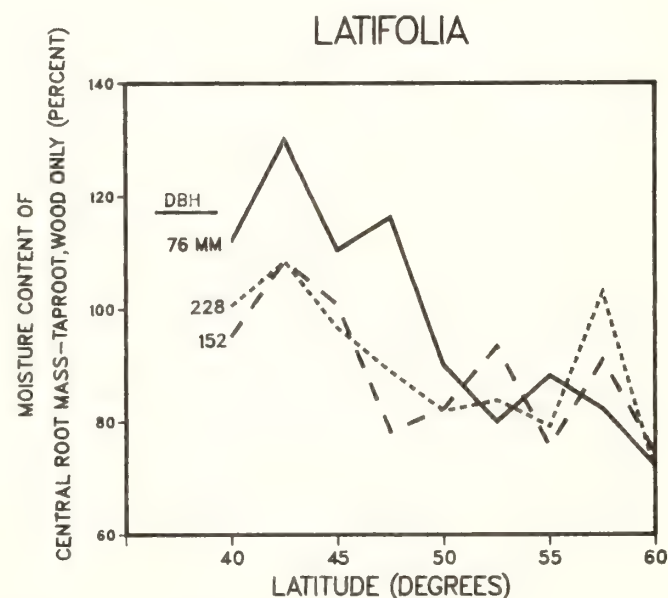


Figure 2-33—Moisture content of the wood in central root mass and taproot related to latitude for *latifolia* trees of three diameters.

Central Root Mass-Taproot, Bark Only

Bark of the central root mass-taproot had average moisture content of 107.1 percent, with standard deviation of 31.5 percentage points. Bark moisture content varied significantly with d.b.h., elevational zone, and latitude. For trees 76, 152, and 228 mm in d.b.h., moisture contents were 121.0 (33.0), 101.6 (31.8), and 98.5 (24.5) percent. Variation with elevational zone was as follows:

Elevational zone	Average moisture content and standard deviation	
	----- Percent -----	
Low	101.0	(33.3)
Medium	106.1	(29.2)
High	114.0	(31.0)

Average bark moisture was highest at 42.5 degrees latitude (145 percent) and lowest at 60 degrees (85 percent) (fig. 2-34).

Correlations between the moisture content of the bark of the central root mass-taproot and the following measured properties are of interest:

Property	r
Specific gravity of complete-tree bark	-0.552
Moisture content of complete-tree bark	.549
Moisture content of stembark at 152 mm stump height	.531
Moisture content of complete tree with cones and foliage	.480
Heartwood volume as percentage of stem-wood volume	-.449
Moisture content of branch-free stem, wood plus bark	.441
Heartwood diameter at 152 mm stump height	-.417

2-6 RESULTS—MURRAYANA

For the *murrayana* trees, the three d.b.h. classes averaged 76 mm with standard deviation of 1.8 mm, 151 mm with standard deviation of 2.9 mm, and 229 mm with standard deviation of 3.9 mm. All were selected at medium elevation, which for the four latitudes averaged as follows (fig. 1-1):

Latitude	Elevation	General location
Degrees	Meters	
37.5	2,402	Just east of Yosemite National Park
40	1,676	Vicinity of Quincy, CA
42.5	2,006	Southwest of Paisley, OR
45	1,148	North of Breitenbush, OR

Because the entire *murrayana* sample totaled but 36 trees, correlations among tree characteristics are not noted in the detail provided for the 243 *latifolia* trees. Standard deviations for diameter-class data are noted in parentheses following their average values, as they were in the *latifolia* results section.

LATIFOLIA

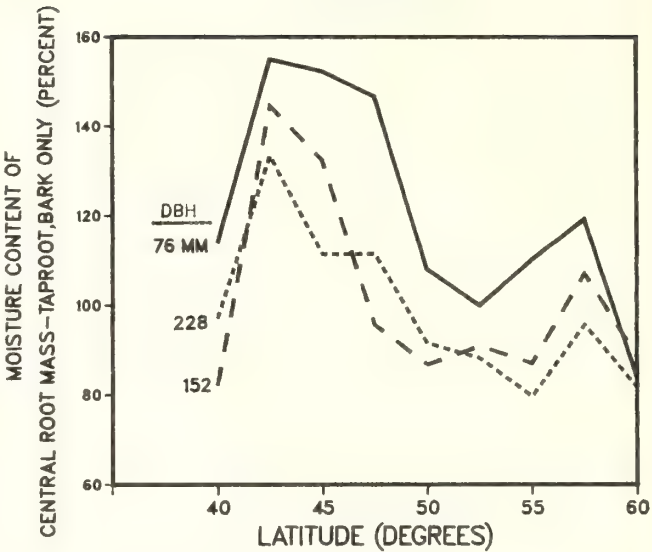


Figure 2-34—Moisture content of the bark of central root mass and taproot related to latitude for *latifolia* trees of three diameters.

Even with this small sample (nine trees per latitude), numerous latitudinal differences were observed. Only those statistically significant are graphed or tabulated. It seems likely from studying the data, however, that had more trees been sampled, statistically significant differences between the two southern latitudes and the two northern latitudes—as well as among diameter classes—would have been found in most of the moisture contents measured.

Complete Tree With Cones and Foliage

Moisture content of complete trees with cones and foliage did not vary significantly with diameter or latitude; the average was 108.6 percent, with standard deviation of 16.6 percent.

Complete Tree Without Cones or Foliage

Average moisture content of complete trees without cones or foliage averaged 108.8 percent, with standard deviation of 17.5 percent. This moisture content did not vary significantly with d.b.h., but was inversely correlated with latitude, as follows:

Latitude	Average and standard deviation	
Degrees	----- Percent -----	
37.5	120.5	(15.7)
40	111.7	(18.1)
42.5	103.4	(8.0)
45	99.5	(20.2)

Complete Tree, Wood Only

Average moisture content of complete-tree wood averaged 108.0 percent, with standard deviation of 19.0 percent; it did not vary significantly with latitude, but was positively correlated with diameter; trees 76, 152, and 228 mm in d.b.h. had tree wood moisture contents of 97.1 (17.4), 111.1 (18.9), and 115.9 (16.6) percent.

Complete Tree, Bark Only

Bark of complete trees had average moisture content of 113.7 percent, with standard deviation of 19.5 percent, but varied significantly (inversely) with both d.b.h. and latitude (fig. 2-35). Treebark in d.b.h. classes of 76, 152, and 228 mm had moisture contents of 124.5 (23.5), 111.2 (14.4), and 105.3 (15.5) percent. Variation with latitude is summarized as follows:

Latitude	Average and standard deviation	
	----- Degrees -----	----- Percent -----
37.5	132.1	(17.6)
40	115.0	(13.8)
42.5	98.4	(10.9)
45	109.1	(19.4)

Foliage

Moisture content of foliage averaged 114.3 percent, with standard deviation of 12.2 percent. It was not significantly related to d.b.h., but did vary significantly with latitude, as follows:

Latitude	Average and standard deviation	
	----- Degrees -----	----- Percent -----
37.5	113.7	(13.6)
40	103.9	(10.3)
42.5	114.5	(2.5)
45	125.1	(9.8)

Cones

Moisture content of cones averaged 22.1 percent, with standard deviation of 20.3 percentage points; neither d.b.h. nor latitude was significantly related to cone moisture content.

Dead Branchwood

As with cones, moisture content of dead branchwood was unrelated to d.b.h. or latitude. With all data pooled, the average moisture content was 16.4 percent, with standard deviation of 6.2 percentage points.

Live Branches, Wood Plus Bark

The moisture content of live branches, wood plus bark, averaged 97.3 percent, with standard deviation of 11.2 percentage points. It was unrelated to latitude, but was positively correlated with d.b.h. classes of 76, 152, and 228 mm as follows: 89.6 (9.8), 98.6 (11.3), and 103.5 (8.2) percent.

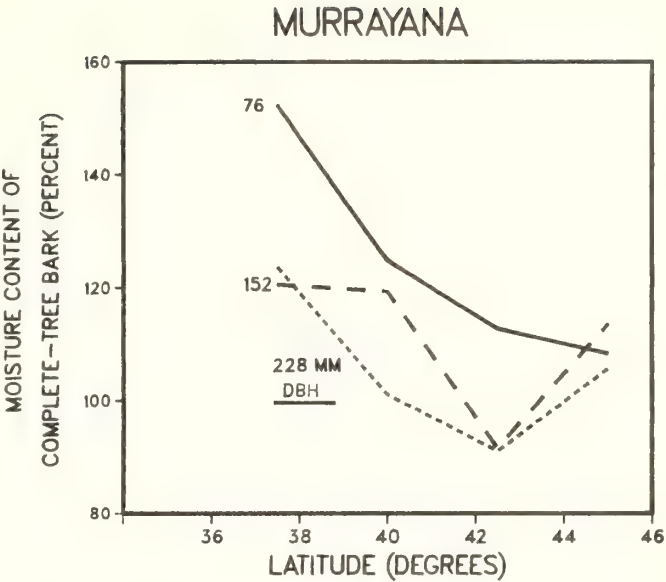


Figure 2-35—Moisture content of complete-tree bark related to latitude for murrayana trees of three diameters.

Live Branchwood

Live branchwood had average moisture content of 92.7 percent, with standard deviation of 12.9 percentage points. It was positively correlated with both d.b.h. and latitude (fig. 2-36). Branchwood moisture content of trees 76, 152, and 228 mm in d.b.h. averaged 82.7 (11.6), 96.5 (13.3), and 98.8 (7.5) percent. Moisture contents averaged least at 37.5 degrees latitude (85 percent) and highest at 42.5 degrees (99 percent).

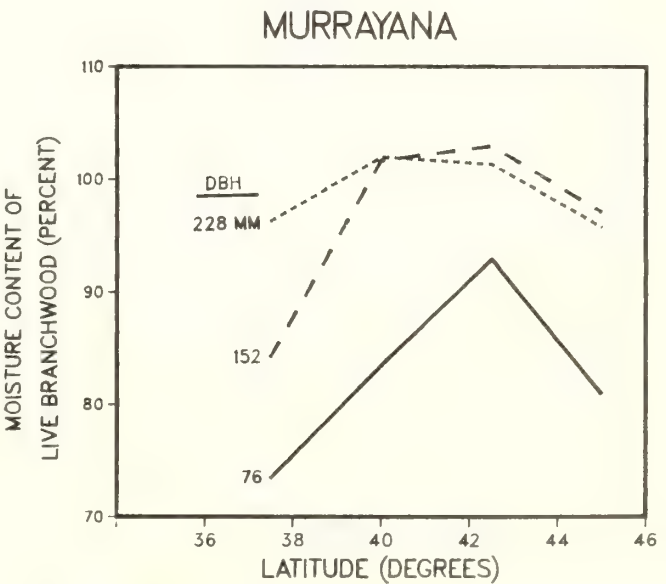


Figure 2-36—Moisture content of live branchwood related to latitude for murrayana trees of three diameters.

Live Branchbark

Live branchbark had average moisture content of 105.3 percent, with standard deviation of 23.8 percentage points; it was positively correlated with d.b.h. and also significantly related to latitude (fig. 2-37). Moisture content of live branchbark from trees 76, 152, and 228 mm in d.b.h. averaged 99.8 (20.2), 101.8 (23.6), and 114.4 (26.5) percent. Bark moisture content was highest at 37.5 degrees latitude (132 percent) and lowest at 42.5 degrees (80 percent).

Stem, Wood Plus Bark—Tree Average

Moisture content of the branch-free stem, wood plus bark, had average moisture content of 111.6 percent, with standard deviation of 19.2 percent. It was unrelated to latitude, but was positively correlated with d.b.h. classes of 76, 152, and 228 mm as follows: 101.8 (17.0), 113.6 (18.9), and 119.4 (18.6) percent.

Stem, Wood Plus Bark—Variation With Height

Moisture content of wood plus bark of branch-free stems increased with increasing height in trees; the three diameter classes had similar moisture content variations with height (fig. 2-38). At 152-mm stump height the average was 98 percent, while at 80 and 90 percent of tree height the average was about 143 percent.

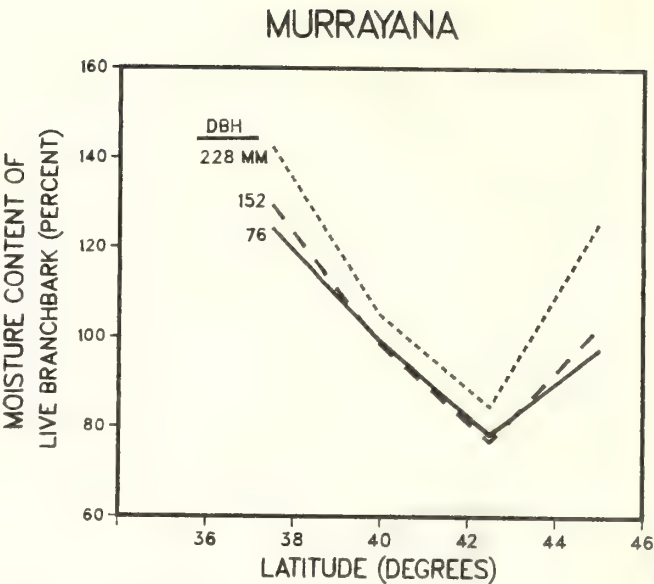


Figure 2-37—Moisture content of live branchbark related to latitude for *murrayana* trees of three diameters.

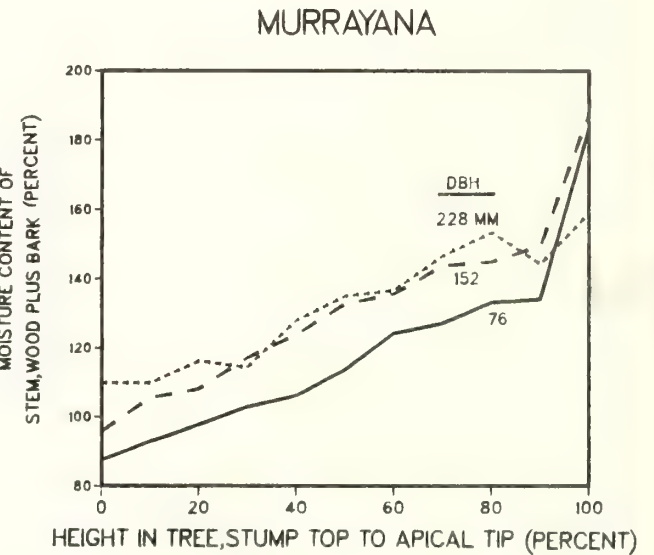


Figure 2-38—Moisture content of branch-free stem, wood plus bark, related to height in tree for *murrayana* trees of three diameters.

Stemwood—Tree Average

Stemwood moisture content averaged 111.2 percent, with standard deviation of 20.9 percent. It was unrelated to latitude, but was positively correlated with d.b.h. classes of 76, 152, and 228 mm as follows: 98.4 (17.4), 113.8 (19.8), and 121.3 (19.8) percent.

Stemwood—Variation With Height

Moisture content of stemwood increased with increasing height in trees; the three d.b.h. classes had similar patterns of variation with height (fig. 2-39). At 152-mm stump height the average was 99 percent, while at 80 percent of tree height average stemwood moisture content was 139 percent.

Stembark—Tree Average

Stembark moisture content averaged 114.1 percent, with standard deviation of 22.6 percentage points. It varied significantly with latitude and also was inversely correlated with d.b.h. (fig. 2-40). Trees 76, 152, and 228 mm in d.b.h. had average stembark moisture contents of 129.3 (26.6), 113.2 (15.7), and 99.9 (14.1) percent. Stembark moisture contents averaged highest at 37.5 degrees latitude (131 percent) and lowest at 42.5 degrees (100 percent).

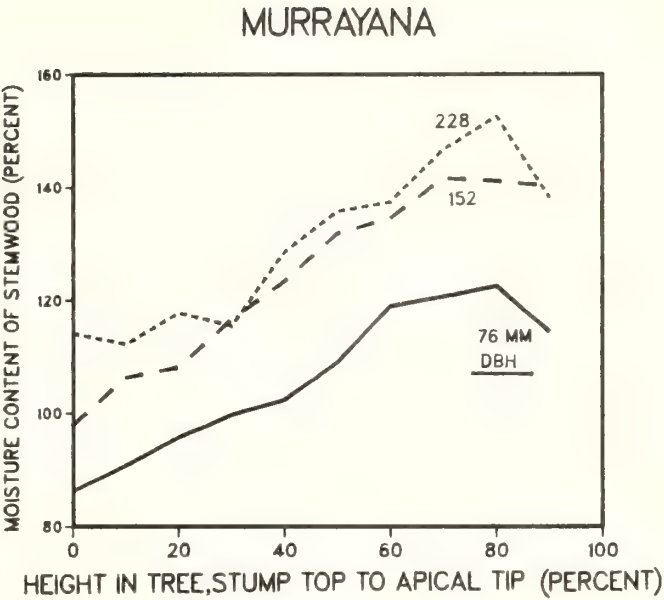


Figure 2-39—Moisture content of stemwood related to height in tree for *murrayana* trees of three diameters.

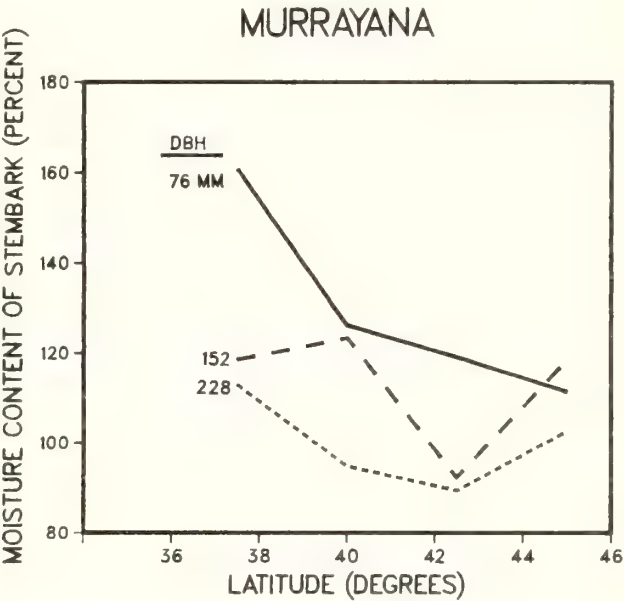


Figure 2-40—Moisture content of stembark related to latitude for *murrayana* trees of three diameters.

Stembark—Variation With Height

Stembark moisture content increased from about 99 percent at stump height to about 131 percent at 90 percent of tree height; patterns of variation with height were similar for the three diameter classes (fig. 2-41). This trend in stembark variation with height in tree was found at all four latitudes studied (fig. 2-42).

Sapwood

Sapwood moisture content averaged 125.1 percent, with standard deviation of 21.2 percentage points. It was unrelated to latitude, but was positively correlated with d.b.h. Trees 76, 152, and 228 mm in diameter had average moisture contents of 104.5 (15.5), 128.5 (14.4), and 142.3 (13.3) percent.

Heartwood

Heartwood moisture content was much less than that of sapwood, averaging 44.4 percent, with standard deviation of 5.8 percentage points. It was unrelated to d.b.h., but varied inversely with latitude, as follows:

Latitude	Average and standard deviation	
Degrees	- - - Percent - - -	
37.5	49.0	(4.7)
40	44.3	(7.7)
42.5	43.4	(4.8)
45	41.1	(2.9)

Stump-Root System, Wood Plus Bark

Wood plus bark of the stump-root system had average moisture content of 112.1 percent, with standard deviation of 22.3 percent. Moisture content was unrelated to d.b.h., but varied inversely with latitude, as follows:

Latitude	Average and standard deviation	
Degrees	- - - Percent - - -	
37.5	126.5	(14.5)
40	119.9	(26.8)
42.5	98.9	(11.9)
45	103.1	(22.8)

Stump-Root System, Wood Only

Moisture content of wood of the stump-root system was unrelated to either d.b.h. or latitude. It averaged 110.8 percent, with standard deviation of 24.3 percentage points.

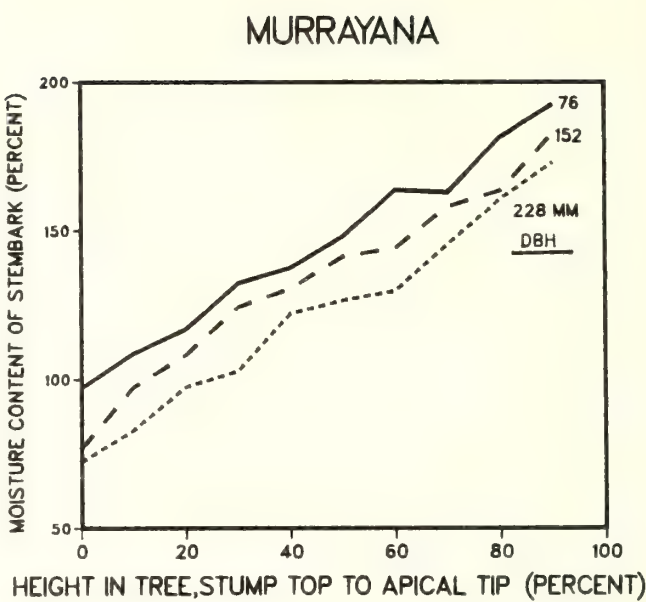


Figure 2-41—Moisture content of stembark related to height in tree for *murrayana* trees of three diameters.

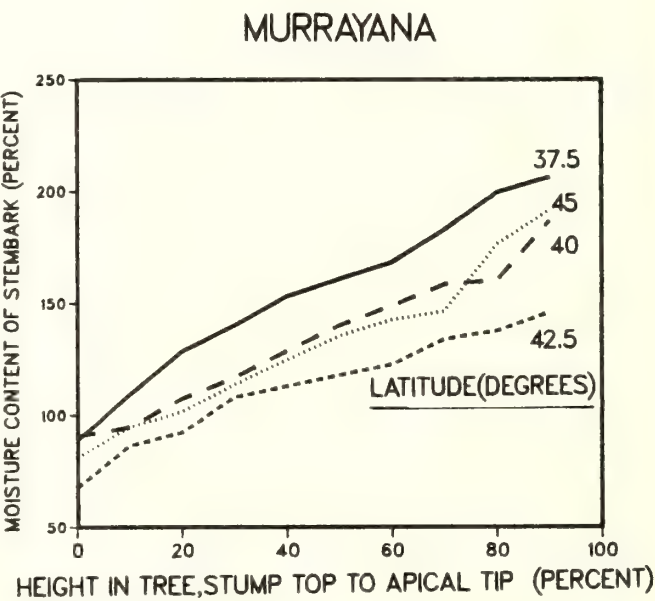


Figure 2-42—Moisture content of stembark related to height in tree and to latitude for *murrayana* trees, with data from the three diameter classes pooled.

Stump-Root System, Bark Only

Bark of the stump-root system had average moisture content of 120.9 percent, with standard deviation of 25.4 percentage points. It varied significantly with both d.b.h. and latitude (fig. 2-43). Bark from 76-mm trees had highest moisture content, averaging 137.4 (28.4) percent; bark from the two larger diameter classes had moisture contents of 111.5 (16.9) and 113.9 (22.7) percent. Bark moisture content was highest at 40 degrees latitude (136 percent) and lowest at 45 degrees (101 percent).

Stump, Wood Plus Bark

Moisture content of wood plus bark of the stump—from groundline to 152 mm stump top—was unrelated to either d.b.h. or latitude. It averaged 99.8 percent, with standard deviation of 22.9 percent.

Stumpwood

Similarly, stumpwood moisture content was unrelated to latitude or d.b.h., averaging 100.7 percent, with standard deviation of 25.5 percentage points.

Stumpbark

Moisture content of stumpbark averaged 92.1 percent, with standard deviation of 29.1 percentage points. It was inversely correlated with both latitude and d.b.h. (fig. 2-44). Trees 76, 152, and 228 mm in d.b.h. had average stumpbark moisture contents of 117.2 (30.3), 84.4 (17.9), and 74.9 (19.7) percent. Moisture content was highest at 37.5 degrees (108 percent) and lowest at 45 degrees (73 percent).

Lateral Roots, Wood Plus Bark

Moisture content of wood plus bark of lateral roots from root collar to 305 mm radius from tree pith averaged 125.1 percent, with standard deviation of 28.0 percentage points. It was unrelated to d.b.h., but varied significantly with latitude, as follows:

Latitude Degrees	Average and standard deviation	
	Percent	Standard Deviation
37.5	142.4	(16.4)
40	136.9	(30.5)
42.5	110.9	(11.3)
45	110.1	(33.7)

Lateral Roots, Wood Only

Moisture content of wood of the lateral roots was unrelated to either d.b.h. or latitude; it averaged 121.4 percent, with standard deviation of 30.5 percentage points.

MURRAYANA

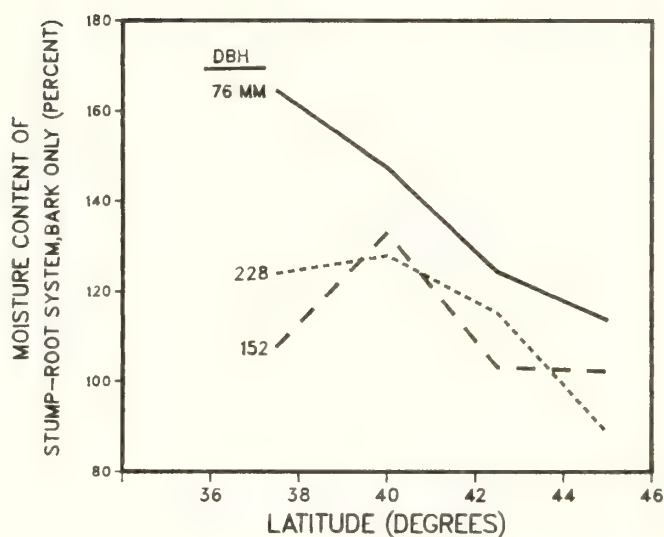


Figure 2-43—Moisture content of bark of the stump-root system related to latitude for *murrayana* trees of three diameters.

MURRAYANA

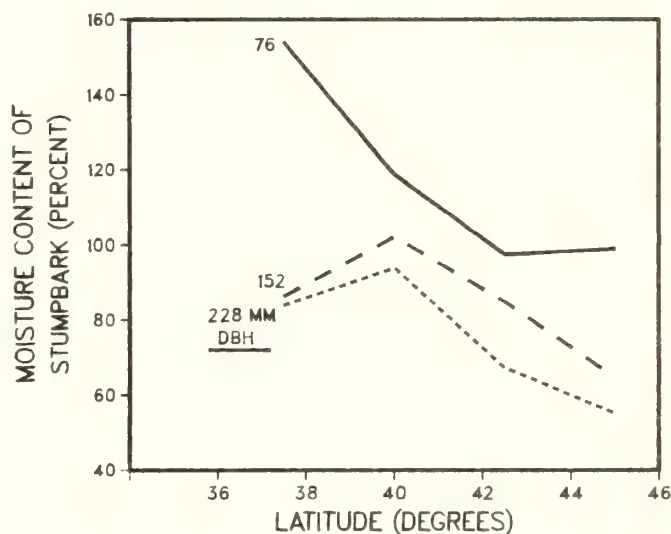


Figure 2-44—Moisture content of stumpbark, groundline to stump top, related to latitude for *murrayana* trees of three diameters.

Lateral Roots, Bark Only

Bark of the lateral roots had moisture content averaging 140.2 percent, with standard deviation of 29.7 percent. It varied inversely with both d.b.h. and latitude (fig. 2-45). Trees 76 mm in d.b.h. had lateral rootbark with moisture content of 158.3 (33.6) percent, whereas those of the two larger diameter classes had moisture contents of 131.2 (23.7) and 131.2 (24.1) percent. Moisture content averaged highest at 40 degrees latitude (157 percent) and lowest at 45 degrees (123 percent).

Central Root Mass-Taproot, Wood Plus Bark

Wood plus bark of the central root mass-taproot—shorn of laterals and stump—had average moisture content of 113.0 percent, with standard deviation of 26.5 percentage points. It was unrelated to d.b.h., but varied significantly with latitude, as follows:

Latitude Degrees	Average and standard deviation	
	Percent	Standard deviation
37.5	126.5	(11.7)
40	124.7	(33.6)
42.5	94.4	(17.0)
45	106.5	(27.0)

Central Root Mass-Taproot, Wood Only

Moisture content of wood of the central root mass-taproot was unrelated to either d.b.h. or latitude; it averaged 112.5 percent, with standard deviation of 28.3 percentage points.

Central Root Mass-Taproot, Bark Only

Bark of the central root mass-taproot had moisture content averaging 115.3 percent, with standard deviation of 34.2 percentage points. It varied significantly with both d.b.h. and latitude (fig. 2-46). Trees 76 mm in d.b.h. had moisture contents averaging 137.6 (30.9) percent, whereas those of the two larger diameter classes averaged 95.6 (34.9) and 112.7 (24.0) percent.

Taproot bark moisture content was highest at 40 degrees latitude (135 percent) and lowest at 45 degrees (98 percent).

MURRAYANA

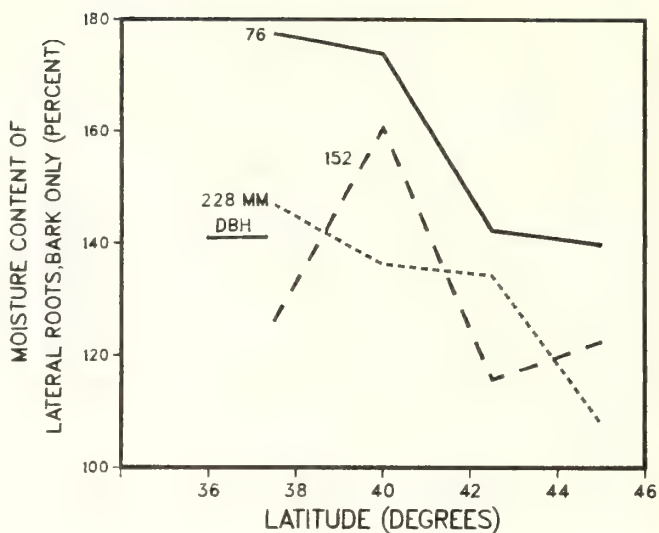


Figure 2-45—Moisture content of bark of lateral roots, root collar to 305 mm radius from tree pith, related to latitude for *murrayana* trees of three diameters.

MURRAYANA

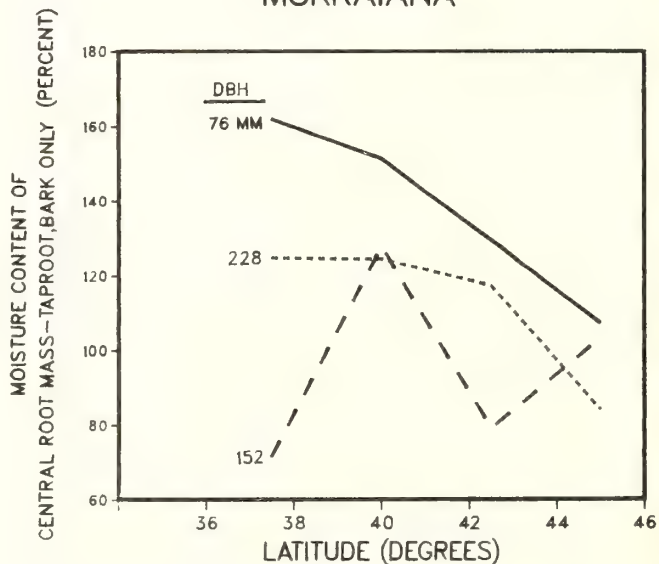


Figure 2-46—Moisture content of bark of central root mass and taproot, shorn of laterals and stump, related to latitude for *murrayana* trees of three diameters.

2-7 RESULTS—LATIFOLIA COMPARED TO MURRAYANA

The experimental design permitted an orthogonal comparison between the two varieties at three latitudes as follows:

- Varieties: (2) *latifolia* and *murrayana*
- D.b.h. classes: (3) 76, 152, and 228 mm
- Latitudinal zones: (3) 40, 42.5, and 45 degrees
- Elevational zones: (1) medium (1,148 to 2,711 m)
- Replications: (3)

Sample size for this comparison therefore totaled 54 trees, 27 of each variety. In the discussions that follow, only significant relationships associated with varietal differences are explained; the other effects are more completely described in the previous two results sections.

No statistically significant varietal differences were observed in moisture contents of the following components:

- Complete tree with cones and foliage
- Complete tree without cones or foliage
- Complete tree, wood only
- Cones
- Live branchwood
- Stem, wood plus bark—tree average
- Stem, wood plus bark—variation with height
- Stemwood—tree average
- Stemwood—variation with height
- Stembark—tree average
- Stembark—variation with height
- Sapwood
- Heartwood
- Stump-root system, wood only
- Stump, wood plus bark
- Stumpwood
- Lateral roots, wood plus bark
- Lateral roots, wood only
- Central root mass-taproot, wood plus bark
- Central root mass-taproot, wood only

Most of the significant varietal differences observed were related to bark and foliage rather than wood moisture content, as discussed in the following paragraphs; dead branchwood was the exception to this generalization.

Foliage

At 40 and 42.5 degrees, *latifolia* had higher foliage moisture contents than *murrayana*; the reverse was true at 45 degrees, as follows:

COMPARISON

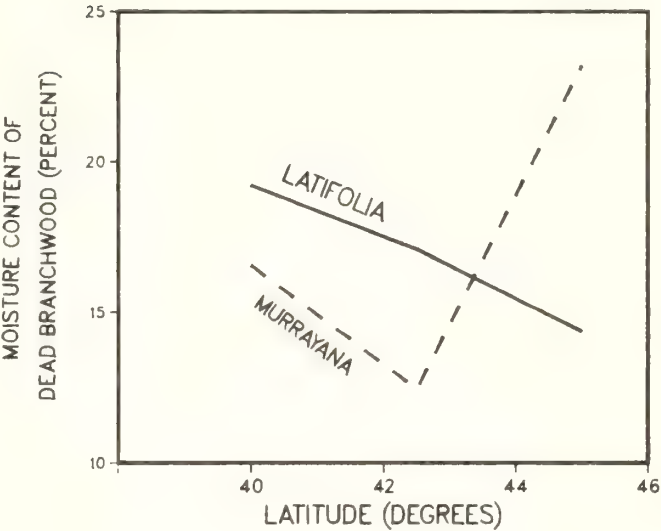


Figure 2-47—Moisture content of dead branchwood of *latifolia* trees of three diameters (diameter data pooled) compared with that of *murrayana* related to latitude.

Latitude	Latifolia		Murrayana	
Degrees	Percent		Percent	
40	120.1	(10.5)	103.8	(10.3)
42.5	119.3	(16.6)	114.5	(2.5)
45	119.7	(14.1)	125.1	(9.8)
Pooled	119.7	(14.1)	114.5	(11.9)

Dead Branchwood

At 40 and 42.5 degrees latitude, *latifolia* had higher dead branchwood moisture content than *murrayana*; the reverse was true at 45 degrees, as follows (fig. 2-47):

Latitude	Latifolia		Murrayana	
Degrees	Percent		Percent	
40	19.2	(5.3)	16.5	(3.2)
42.5	17.1	(3.1)	12.4	(1.2)
45	14.4	(1.6)	23.2	(8.7)
Pooled	16.9	(4.1)	17.4	(6.9)

Live Branches, Wood Plus Bark

The moisture content of wood plus bark of live branches was significantly higher in *latifolia* than in *murrayana*, as follows:

D.b.h.	<i>Latifolia</i>		<i>Murrayana</i>	
mm	----- Percent -----			
76	100.3	(13.7)	88.6	(11.0)
152	106.1	(6.8)	97.7	(11.0)
228	107.7	(20.3)	101.2	(8.0)
Pooled	104.7	(14.5)	95.8	(11.1)

Live Branchbark

Moisture content of the bark of live branches was also significantly higher in *latifolia* than in *murrayana* trees, as follows (fig. 2-48):

D.b.h.	<i>Latifolia</i>		<i>Murrayana</i>	
<i>mm</i>	----- Percent -----			
76	115.3	(21.6)	91.6	(16.0)
152	120.0	(32.6)	92.6	(15.6)
228	121.3	(22.9)	105.2	(20.0)
Pooled	118.9	(25.2)	96.5	(17.8)

Stump-Root System, Wood Plus Bark

Moisture content of wood plus bark of the stump-root system averaged higher in *latifolia* (110.8 percent, with standard deviation of 21.6 percentage points) than in *murrayana* (107.3 percent, with standard deviation of 22.6 percentage points), but this was due only to a large difference at 42.5 degrees latitude; at 40 degrees and 45 degrees the reverse was true (fig. 2-49).

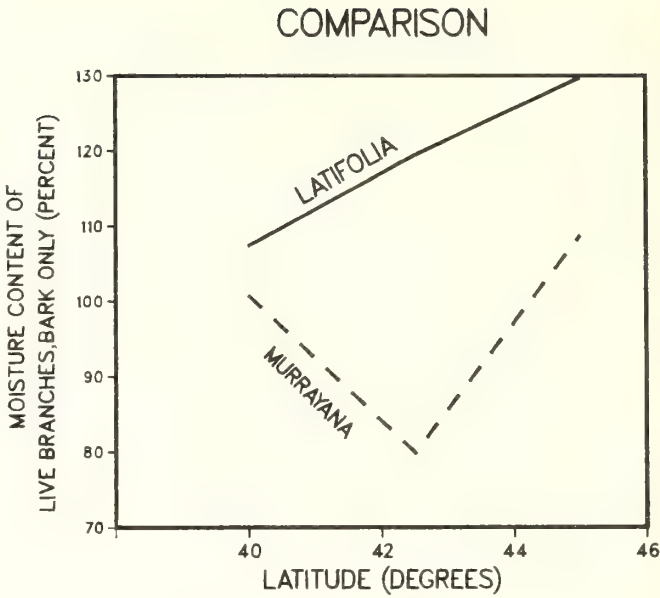


Figure 2-48—Comparative moisture content of live branchbark of *latifolia* and *murrayana* trees of three diameters (diameter data pooled) related to latitude.

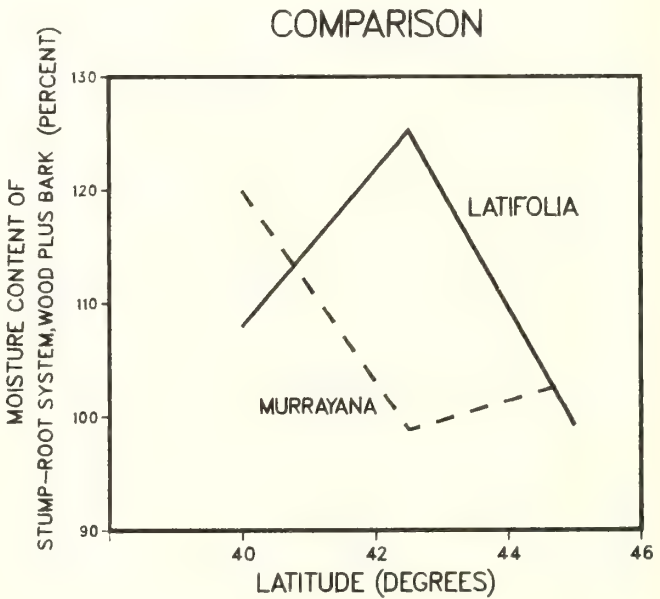


Figure 2-49—Comparative moisture content of stump-root system, wood plus bark, of *latifolia* and *murrayana* trees of three diameters (diameter data pooled) related to latitude.

Stump-Root System, Bark Only

Moisture content of bark of the stump-root system of *latifolia* averaged 128.3 (27.8) percent, while that of *murrayana* was less at 117.2 (23.3) percent, but this relationship reversed at 40 degrees latitude in trees of the two larger diameter classes (fig. 2-50).

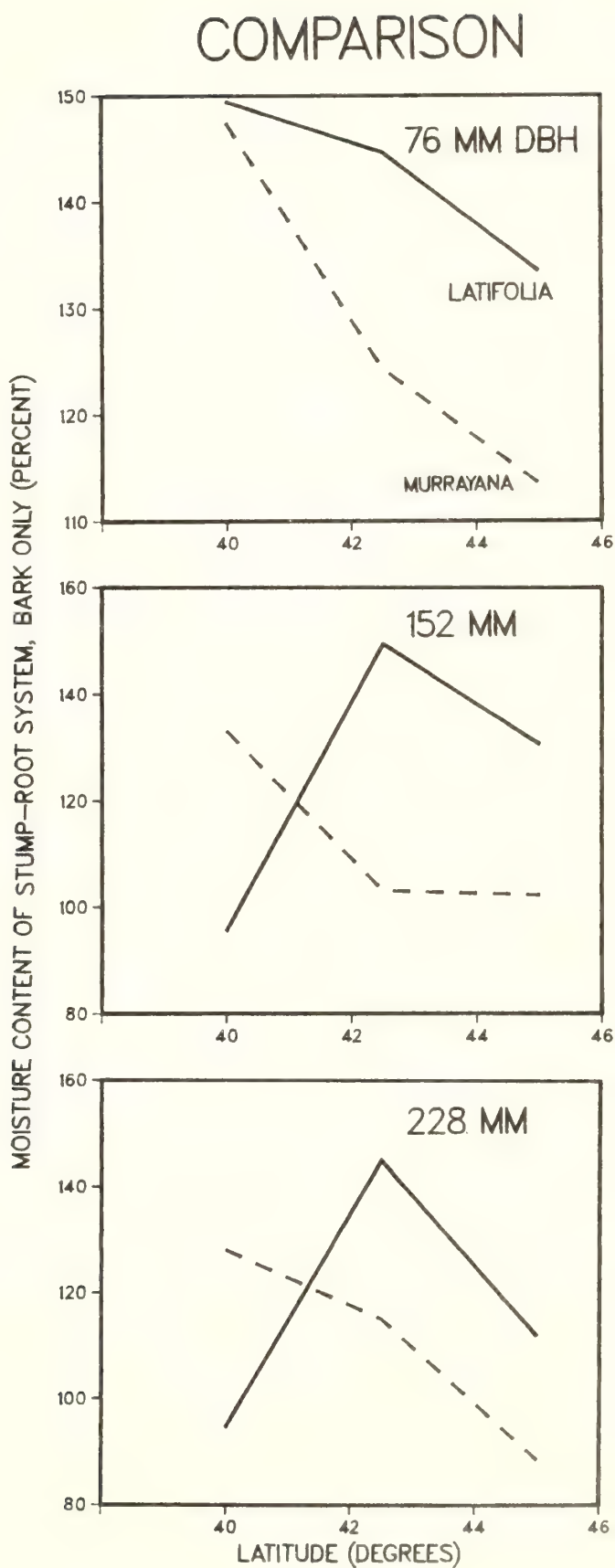


Figure 2-50—Comparative moisture content of stump-root system bark of *latifolia* and *murrayana* trees of three diameters related to latitude.

Stumpbark

The stumpbark of both *latifolia* and *murrayana* had average moisture content of 87 percent, but variety moisture contents differed significantly with various combinations of latitude and diameter class (fig. 2-51).

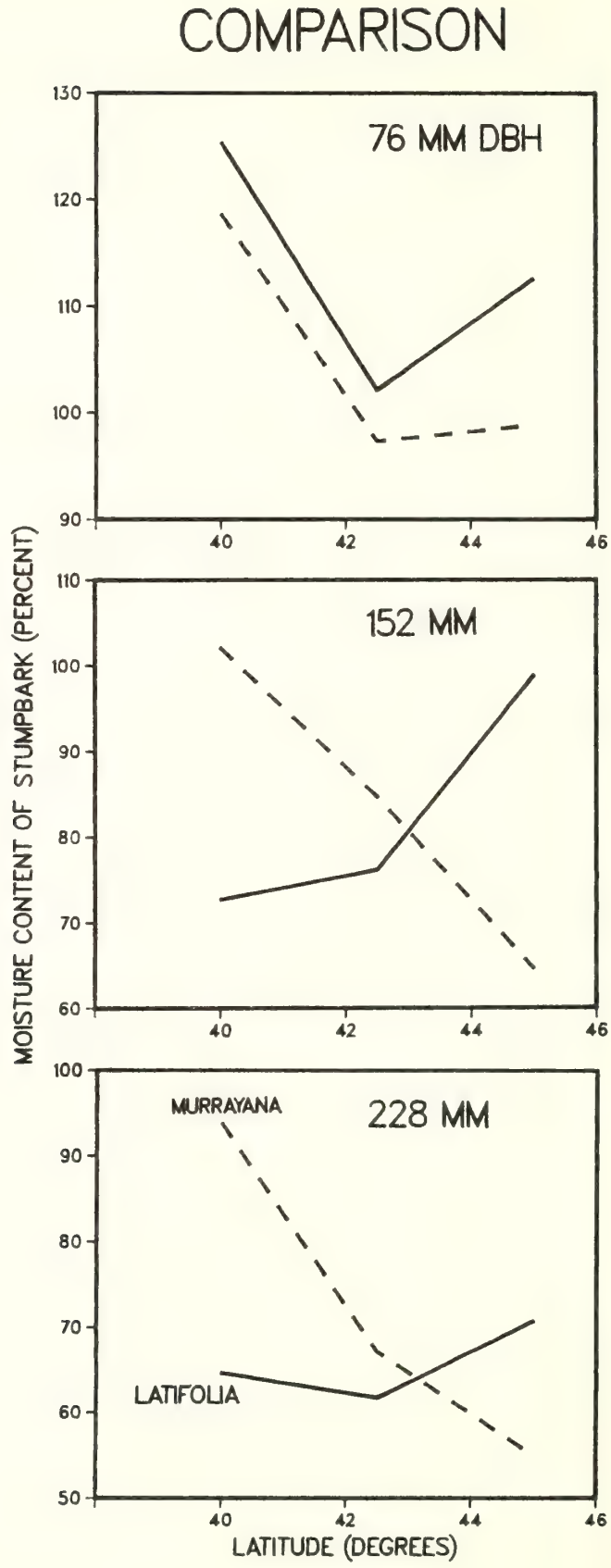


Figure 2-51—Comparative moisture content of stumpbark of *latifolia* and *murrayana* trees of three diameters related to latitude.

Lateral Roots, Bark Only

Bark of the lateral roots of *latifolia* had average moisture content of 104.7 (27.3) percent—less than the average for *murrayana*, which was 108.5 (28.7) percent; but this relationship changed depending on latitude and diameter class (fig. 2-52).

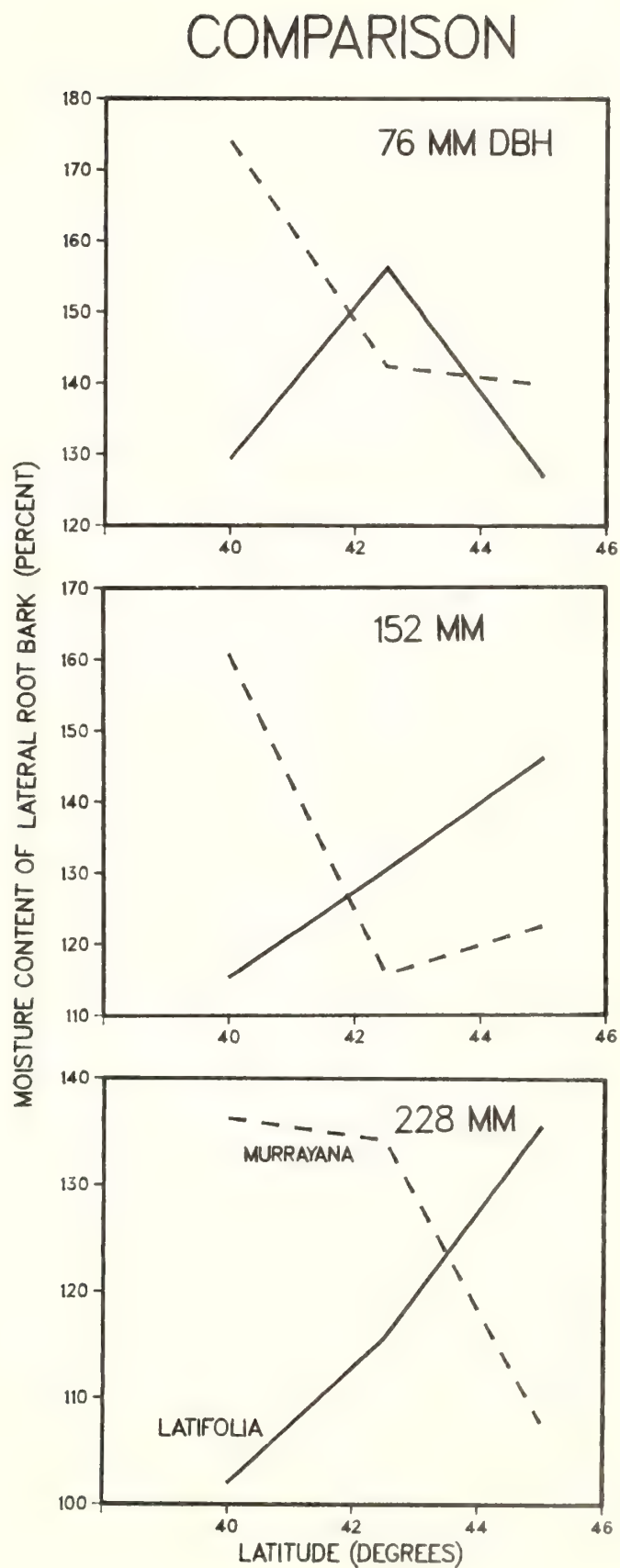


Figure 2-52—Comparative moisture content of lateral root bark of *latifolia* and *murrayana* trees of three diameters related to latitude.

Central Root Mass-Taproot, Bark Only

Bark of the central root mass-taproot of *latifolia* had average moisture content of 123.4 (25.7) percent—more than the average for *murrayana* which was 113.9 (28.7); but this relationship reversed at 40 degrees latitude (fig. 2-53).

For those bark components where significant differences in moisture content were observed, moisture of *latifolia* bark tended to be positively correlated with latitude, whereas bark moisture of *murrayana* tended to be negatively correlated with latitude.

2-8 SUMMARY OF RESULTS

The moisture contents of components of lodgepole pine trees of varieties *latifolia* and *murrayana* are strongly related to latitude and diameter, but less related to elevational zone. Longitudinal zone was studied only for *latifolia*, but no effects were discernible.

Differences between the moisture contents of tree components of *latifolia* and *murrayana* were minor—most related to bark moisture contents; in latitudes 40, 42.5, and 45 degrees *latifolia* bark moisture content tended to be positively correlated with latitude, whereas bark moisture of *murrayana* was negatively correlated with latitude.

Throughout the full range of latitude (40 to 60 degrees) in which *latifolia* moisture contents were studied, however, there was a pronounced decrease in *latifolia* tree-component moisture content from south to north. Maximum moisture contents usually occurred at latitude 42.5 or 45 degrees, and minimums were observed between 52.5 and 60 degrees. For example, stemwood moisture content (diameter data pooled) averaged 124 percent at 42.5 degrees and only 83 percent at 60 degrees. Similarly, stembark moisture content averaged 131 percent at 45 degrees but only 80 percent at 52.5 degrees.

Moisture contents of the following components were inversely correlated with d.b.h., that is, moisture contents were higher in trees 76 mm in d.b.h. than in trees of larger diameter: complete trees (with or without foliage), foliage, stembark, heartwood, and wood and bark of the stump-root system. Sapwood, however, had higher moisture content in trees of large diameter than in those of small diameter.

The moisture content of both wood and bark increased sharply from stump height to upper stem; the increase was greater in bark (72 to 165 percent) than in wood (90 to 130 percent).

Moisture contents of tree components were most closely and most frequently correlated with specific gravity of wood and bark of components, heartwood percentage of stemwood volume, sapwood thickness at stump height, and with crown ratio.

Tree-average moisture contents (all *latifolia* data pooled) for tree components were generally in the range from 90 to 110 percent of oven-dry weight, with exceptions as follows: cones (26 percent), dead branchwood (18 percent),

COMPARISON

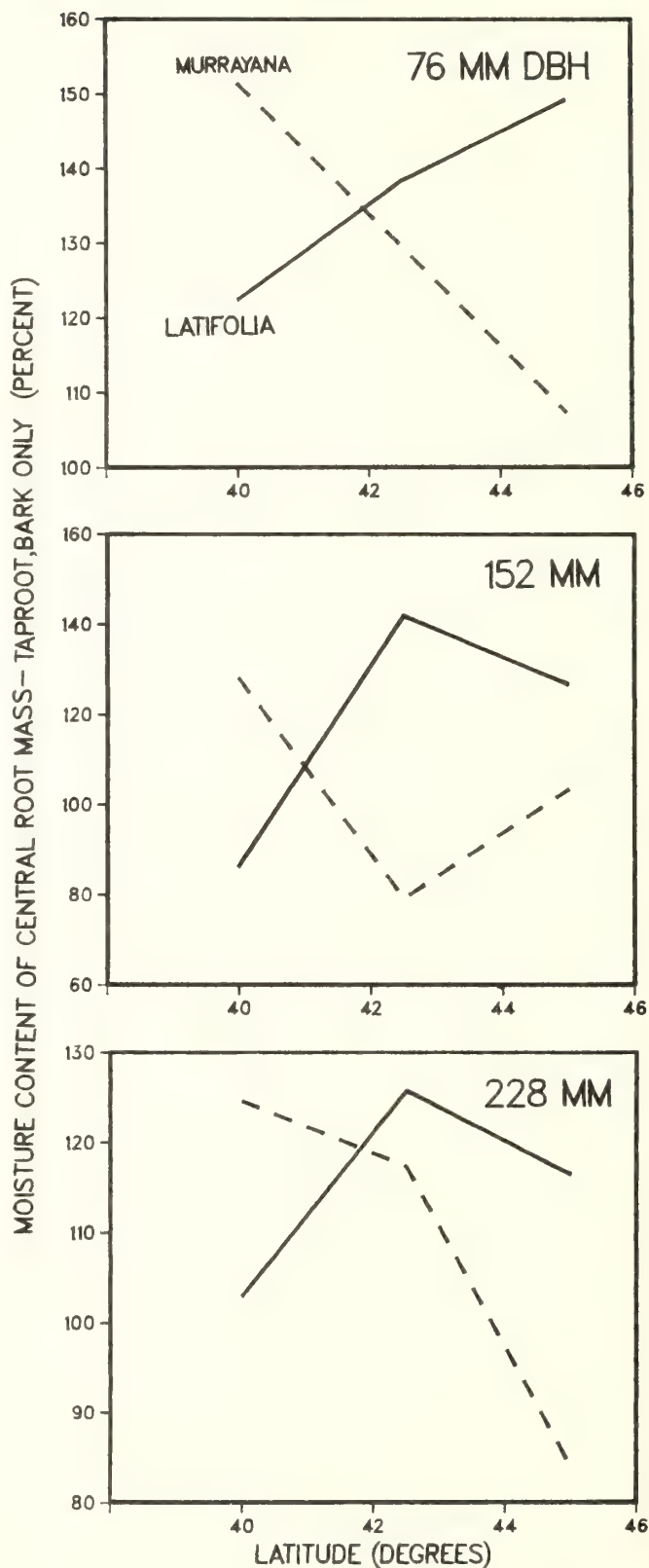


Figure 2-53—Comparative moisture content of bark from the central root mass-taproot of *latifolia* and *murrayana* trees of three diameters related to latitude.

sapwood (119 percent), heartwood (43 percent), and bark of lateral roots (121 percent).

Significant variations related to latitude, d.b.h., elevational zone, and height in tree are so large, however, that variety-wide generalizations about average moisture contents of tree components should be made with caution.

2-9 REFERENCES

- Brown, James K. Weight and density of crowns of Rocky Mountain conifers. Research Paper INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1978. 56 p.
- Dixon, Hobart Norris. The growth of lodgepole pine in the Colorado front range as related to environment. Dissertation Abstracts International. 30(6): 2561-B; 1969. Abstract.
- Dobie, J.; McIntosh, J. A. Spruce foliage yields more than triple that of pine. Pulp and Paper of Canada. 77(10): 71-72; 1976.
- Fahey, Thomas D. Evaluating dead lodgepole pine for products. Forest Products Journal. 30(12): 34-39; 1980.
- Fahey, Thomas D. Value ranking for utilizing lodgepole pine residues. In: Harvesting and utilization opportunities for forest residues in the Northern Rocky Mountains: symposium proceedings; 1979 November 28-30; Missoula, MT. General Technical Report INT-110. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981: 239-250.
- Fahnestock, George R. Logging slash flammability. Research Paper 58. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1960. 67 p.
- Ince, Peter J. Economic perspective on harvesting and physical constraints on utilizing small, dead lodgepole pine. Forest Products Journal. 32(11/12): 61-66; 1982.
- Johnstone, W. D. Some variations in specific gravity and moisture content of 100-year-old lodgepole pine trees. Information Report A-X-29. Calgary, AB: Department of Fisheries and Forestry, Canadian Forestry Service, Forest Research Laboratory; 1970. 19 p.
- Lieu, Peter J.; Kelsey, Rick G.; Shafizadeh, Fred. Some chemical characteristics of green and dead lodgepole pine and western white pine. Research Note INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 8 p.
- Lowery, David P. Using dead softwood timber: kiln-drying procedures for lumber and preservative treatments for fenceposts. In: The dead softwood timber resource: Proceedings; 1978 May 22-24; Spokane, WA. Pullman, WA: Washington State University; 1978: 127-146.
- Lowery, David P.; Hearst, Allen L., Jr. Moisture content of lumber produced from dead western white pine and lodgepole pine trees. Research Paper INT-212. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1978. 11 p.
- Lowery, David P.; Hillstrom, William A.; Elert, Erwin E. Chipping and pulping dead trees of four Rocky Mountain timber species. Research Paper INT-193. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 11 p.
- Markstrom, Donald C.; Hann, Robert A. Seasonal variation in wood permeability and stem moisture content of three Rocky Mountain softwoods. Research Note RM-212. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1972. 7 p.
- Reid, R. W. Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. Forestry Chronicle. 37(4): 368-375, 403; 1961.
- Smith, J. H. G.; Kozak, A. Thickness, moisture content, and specific gravity of inner and outer bark of some Pacific Northwest trees. Forest Products Journal. 21(2): 38-40; 1971.
- U.S. Department of Agriculture, Forest Service. Commercial and laboratory pulping tests were made on insect-killed and green-cut lodgepole pine. In: Thirty-seventh annual report for the calendar year 1947. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Rocky Mountain Forest and Range Experiment Station; 1948: 22-23.

CHAPTER 3: STEM TAPER

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3-1 INTRODUCTION

Taper of trees strongly affects their utility. Stems with little taper are preferred in roundwood products, yield more lumber when sawn, and contain more cubic volume when chipped for fiber than those of the same butt diameter but with a high degree of taper. Among coniferous species lodgepole pine is noted for its minimal taper; it does, however, display significant variation in this characteristic.

3-2 OBJECTIVE AND SCOPE

Only those taper parameters most important to processors of lodgepole pine stems are scrutinized in this chapter, and no attempt is made to construct equations predicting stem form; instead, graphs are presented of data aggregated in various significant ways that permit reading of taper information directly from the observed study data. Emphasis is given to stem dimensions inside bark below the live crown as distinct from stemwood within the live crown. Because processors frequently leave whole crowns in the forest, it is useful to know the percentage of total stemwood such crown stemwood represents, and the diameter of stemwood at the base of the live crown. Also, stem forms are plotted to illustrate their curvilinearity with height in tree.

As previously noted, the characterization effort is confined to two varieties of lodgepole pine: *Pinus contorta* var. *latifolia* Engelm. and *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm., with emphasis on the former. The primary objective during tree collection was to obtain three replications of disease- and insect-free specimens of var. *latifolia* measuring 76, 152, and 228 mm in diameter at breast height (d.b.h.) at low, medium, and high elevations from nine equally spaced north latitudinal zones (40 to 60 degrees) across 10 degrees of longitude in such a way as to encompass the major range of this variety (fig. 1-1).

A secondary objective was to sample three replications of these same three diameter classes of var. *murrayana* at midelevation at four north latitudes (37.5, 40, 42.5, and 45 degrees) in California and Oregon at a single longitude per latitude (fig. 1-1).

The trees of both varieties were sampled in such a way that between-variety comparisons could be made for mid-elevation trees at latitudes 40, 42.5, and 45 degrees. The sampling plan does not permit computation of species-average values. The collection totaled 243 *latifolia* and 36 *murrayana* trees.

Explanations of statistical analyses procedures and a table of analyses of variance formats, with degrees of freedom indicated, are shown in table 1-2. In the results portion of this chapter standard deviations are noted in the text in parentheses following average values. Correlations of interest observed in *latifolia* between taper data and tree characteristics are also noted in the results section of the chapter.

3-3 LITERATURE REVIEW

In his treatise on *latifolia* in Alberta, Smithers (1961) commented on its variability in form of bole. He noted that boles of open-grown trees taper noticeably in an almost conical form. In extremely dense stands the stem is whiplike and hardly thicker at ground level than at the top; he also found this stem form in muskeg and other high-water-table conditions where growing conditions are submarginal. Smithers further observed that in more mature stands density affects appearance, so that in very dense stands (for example, 25,000 stems per ha at 90 years) trees have very little taper and are rarely over 6 m in height and 76 mm in d.b.h. At medium densities (2,500 to 7,500 stems per ha), form class is usually high, averaging 70 to 75 percent. In low-density stands (250 to 1,500 mature trees per ha) the bole has considerably more taper and form class is usually 65 to 70 percent. (Form class is the ratio between d.b.h. outside bark and the diameter inside bark at the top of the first 16-ft log.)

Baranyay and Safranyik (1970) found that stem taper is also related to growth modification caused by dwarf mistletoe attack; heavily infected trees had greater taper than those of uninfected Alberta stands of *latifolia*.

Plank and Cahill (1984) observed that coniferous trees have a stem comprised of many different shapes (fig. 3-1), and selection of an accurate and unbiased formula to estimate the cubic volume of tree-length logs is therefore difficult. To evaluate the performance of three commonly used formulas for estimating cubic volume, they sampled 509 lodgepole pine tree-length logs (inside bark) from Wyoming and Oregon. They found that Smalian's formula overestimated volume by 19 percent, Bruce's formula

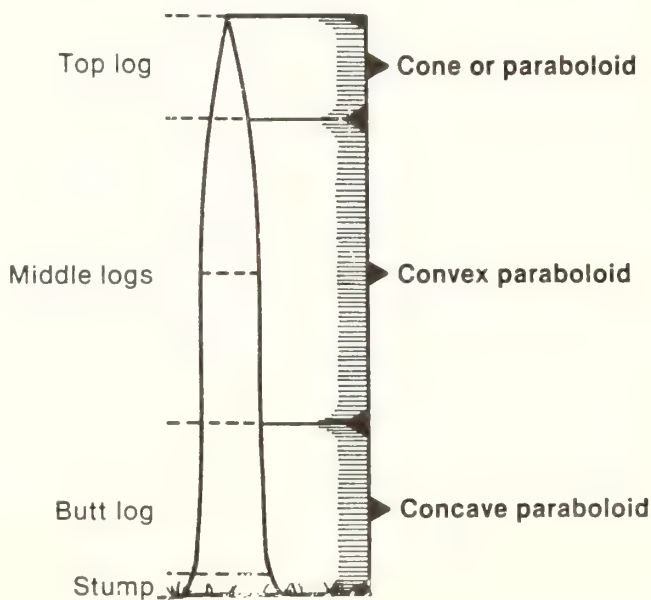


Figure 3-1—Geometric shapes in a coniferous tree stem. (Drawing from Plank and Cahill 1984.)

underestimated by 16 percent, and Huber's formula underestimated by 2 percent. They recommended Huber's formula, which follows:

$$\text{Volume in cubic feet} = 0.005454(D^2)L$$

where:

- D = diameter at midlength of log, inches
- L = log length, feet.

It is beyond the scope of this paper to delve deeply into the mathematical formulation of stem curves; those interested in the subject will find useful the review by Sterba (1980).

Following are a few abstracts of additional North American literature specific to taper in lodgepole pine.

In 1973 Adamovich (1975a) sampled *latifolia* 113 km north of Prince George, BC, from relatively open, mixed stands on optimum growing sites at low elevation where tree crowns had high green weight. In 1974 he also sampled *latifolia* on poor sites in British Columbia at elevations from 730 m to 1,460 m in the vicinities of Cranbrook, Penticton, Kamloops, Prince George, and Burns Lake (Adamovich 1975b). He expressed the taper in stems studied as the ratio of section butt diameters outside bark to breast height diameter outside bark. In the following tabulation, the values opposite decile 1 mean the ratio of stump diameter to d.b.h.; the values opposite decile 5 mean the ratio of the butt diameter of a log, with length of one-tenth of tree height and small end at 50 percent of tree height, to d.b.h. Values in parentheses in the "poor site" column are standard deviations, as follows:

Decile	Good site	Poor site
	----- Ratio -----	
1	1.46	1.18 (.07)
2	.96	.98 (.03)
3	.88	.92 (.03)
4	.82	.87 (.04)
5	.77	.79 (.04)
6	.71	.73 (.05)
7	.65	.65 (.05)
8	.57	.55 (.07)
9	.44	.44 (.07)
10	.23	.28 (.08)

These data indicate that taper within the first tenth of tree height (including butt swell just above the stump) is greater on good sites than on poor sites.

Alemdag and Honer (1977) tabulated the relationship between breast height and stump diameters—both measured outside bark—for *latifolia* in central and eastern Canada; their data are abstracted as follows:

D.b.h.	Diameter of stump at four stump heights			
	10 cm	20 cm	30 cm	60 cm
<i>mm</i>	----- Millimeters -----			
100	118	115	113	107
140	165	161	158	150
180	212	207	203	193
220	259	253	248	236
260	306	299	293	279

Ziegler (1907) tabulated similar data, but in feet and inches, for *latifolia* from the Medicine Bow National Forest in Wyoming, as follows:

D.b.h.	Diameter of stump (outside bark) at three stump heights		
	1 foot	2 feet	3 feet
<i>Inches</i>	----- Inches -----		
5	5.5	5.4	5.2
6	6.6	6.4	6.2
7	7.8	7.4	7.2
8	8.9	8.4	8.2
9	10.0	9.4	9.2
10	11.1	10.4	10.2

Gideon and Faurot (1977) developed a model for *latifolia* predicting merchantable length; that is, length of bole from stump top to a predetermined inside-bark top diameter, excluding trimming allowance. Their formula requires knowledge only of d.b.h. and tree height, as follows:

$$y = (b_3 + b_4h_1) (x - b_2)^{b_1} / [1 + (b_3 + b_4h_1) (x - b_2)^{b_1} / h]$$

where:

- y = merchantable length, feet
- h = total tree height, feet
- $h_1 = (h - h_m) / h$
- x = d.b.h., inches
- b_2 = top diameter limit, inches

Other constants, related to the top diameter limit, as follows:

Top diameter limit	b_1	b_3	b_4	h_m
<i>Inches</i>				<i>Feet</i>
2	0.97	6.82	87.02	21.0
3	.95	3.84	71.14	24.0
4	.86	2.26	70.83	28.0
5	.77	1.65	78.06	36.0
6	.80	5.41	62.96	44.0
7	.86	8.95	42.40	51.0
8	.93	5.98	33.71	51.0

In this equation, h_m is the total height of the shortest tree within a species for a particular top diameter. When evaluated against measurements of western Montana *latifolia* trees, R^2 values ranged from 0.88 to 0.99, with standard error of estimates from 2.0 to 4.7 feet; predictions of merchantable length were most accurate with small top diameter limits.

Hanzlik (1916) provided taper tables for *latifolia* trees in the Ochoco National Forest on a western spur of the Blue Mountains of eastern Oregon. He tabulated inside bark diameters at various heights above ground for trees 7 through 20 inches in d.b.h., stratified by tree heights; that is, less than 60 feet, 61 to 80 feet, and more than 80 feet.

For Colorado and Wyoming *latifolia* trees, Myers (1964) related inside bark diameters at various heights above ground for trees 3.5 to 25.5 inches d.b.h. outside bark, stratified by tree height classes of 30, 40, 50, 60, 70, 80, and 90 feet.

Heger (1965) used Hohenadl's method on 37 dominant and codominant *latifolia* trees grown on various sites in the Clearwater District of Alberta. He concluded that the method efficiently and accurately estimated stem form and stem volume. He also concluded that for 80 percent of the lower bole of *latifolia*, stem form (over bark) in Alberta does not differ appreciably from stem form (bark-free) in British Columbia.

MacLean and Berger (1976) determined the form factor—the ratio of tree cubic volume to that of a cylinder with the same diameter and length—for *murrayana* in California, as follows:

$$F = 0.422709 - 0.0000612236 (H^2/D)$$

where:

F = form factor as defined above

H = tree height, feet

D = d.b.h., feet.

3-4 PROCEDURE

Procedural details of the study are given in chapter 1, and will not be repeated here except to note that the diameters of the larger stem disks taken at 10 percent height intervals were measured in the laboratory with a diameter tape—both inside and outside bark. The smaller disks were measured with a scale on major and minor diameters and values averaged.

Average inside bark stem taper below crown, expressed as millimeters taper per meter of stem length below crown, was calculated by considering the below-crown stem section as a truncated cone with bottom diameter equal to diameter at 152-mm stump height and top diameter equal to the diameter of the stem at the base of the live crown. Within-crown taper was calculated by considering this stem portion as a cone with bottom diameter equal to inside bark stem diameter at the base of the live crown and top diameter of zero at the apical tip.

The elevational zones of low, medium, and high are relative. Medium refers to an elevation that is medium for the variety at the latitude at which sampled; similarly, low and high refer to lower and upper elevational zones in which the variety occurs at the latitude sampled. *Latifolia* elevational zones were highest in the south (2,481, 2,711, and 3,144 m at 40 degrees) and progressively lower with each more northerly latitude (604, 739, and 879 m at 60 degrees). *Murrayana* was sampled at elevations in the range from 1,148 to 2,402 m.

Trees were taken from within natural unthinned stands on level benches in National or Provincial Forests. The

sampling scheme resulted in selection of 76-, 152-, and 228-mm trees averaging 71, 91, and 107 years of age, respectively, for *latifolia*, and 67, 84, and 91 years for *murrayana*. Most of the small-diameter trees were suppressed, while the larger trees were the fast growers.

3-5 RESULTS—LATIFOLIA

Average taper data are summarized in table 3-1, but interpretation of these averages requires reference to the main effects and interactions related to d.b.h., latitude, and elevational zone—as discussed in the following paragraphs.

In the following paragraphs summarizing results, only those main effects and interactions shown statistically significant (0.05 level) by analyses of variance are discussed, tabulated, and graphed. All reported conclusions are statistically significant (0.05 level).

As noted previously (fig. 1-1), latitudinal sampling spanned 10 degrees of longitude. The only significant taper-related variation associated with longitudinal zone was that of within-crown taper; the correlation was weak (*r* = -0.189), indicating that within each latitudinal zone, trees on the western end had slightly less within-crown taper than those on the eastern end.

Table 3-1—Average values (and standard deviations) of taper-related data for 243 *latifolia* and 36 *murrayana* trees aggregated by variety¹

Statistic	Variety	
	<i>Latifolia</i>	<i>Murrayana</i>
Average stem taper from 152-mm stump height to base of live crown, inside bark (mm/m)	8.2 (3.6)	9.5 (4.7)
Average stem taper from base of live crown to apical tip, inside bark (mm/m)	15.8 (4.1)	15.7 (4.8)
Stem diameter at base of live crown, inside bark (mm)	100.1 (43.5)	111.8 (48.8)
Stemwood volume within live crown, proportion of total stemwood volume from 152-mm stump height to apical tip (percent)	16.0 (12.1)	26.5 (13.8)

¹Because of significant variations related to d.b.h., latitude, and elevational zone, reference to appropriate figures and test discussion is required for interpretation of these data.

Stem Form

As previously noted, coniferous trees typically display three different geometric shapes from stump top to apical tip (fig. 3-1). For simplicity, inside bark stem forms of 76-, 152-, and 228-mm *latifolia* trees from low-, medium-, and high-elevation zones are shown (figs. 3-2, 3-3, and 3-4) divided into only two segments—that between stump top and base of the live crown, and that within the live crown. It is evident that average stemwood taper is significantly greater within the crown than below the crown.

LATIFOLIA LOW ELEVATION

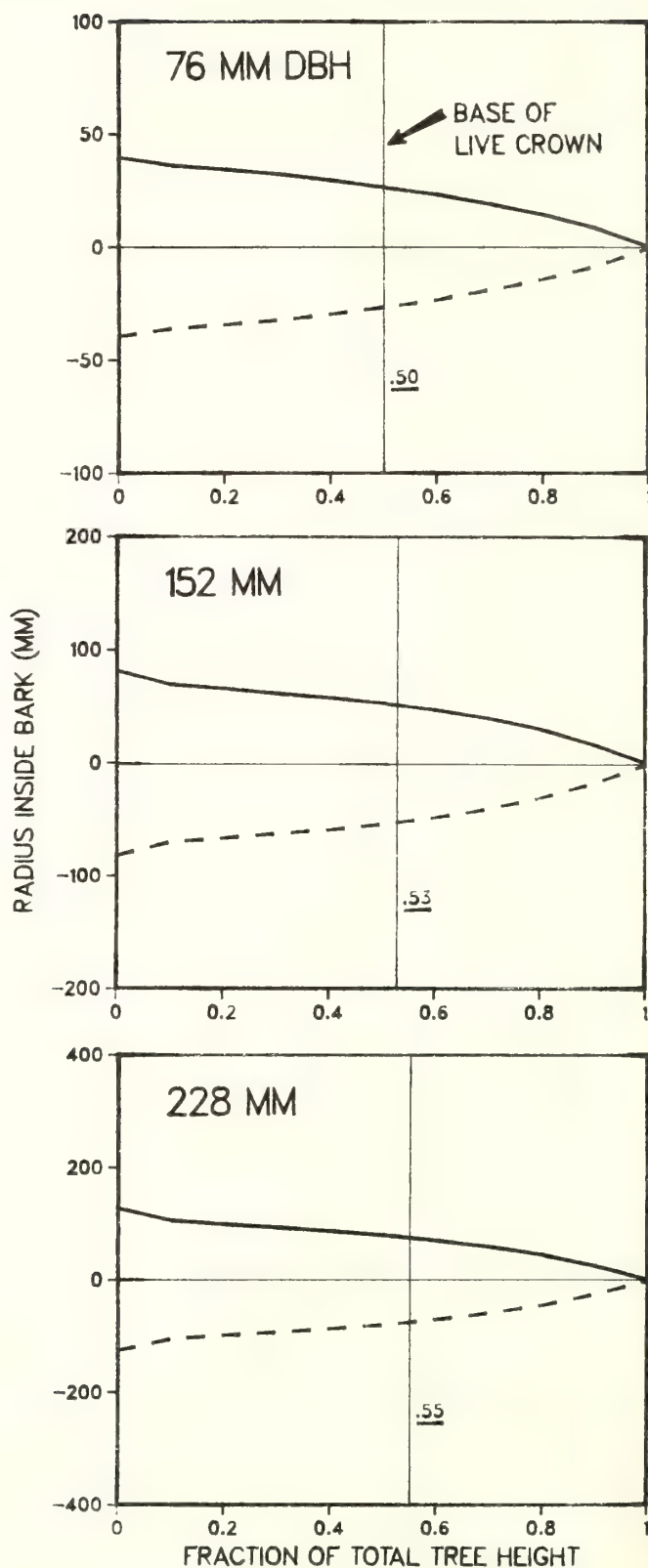
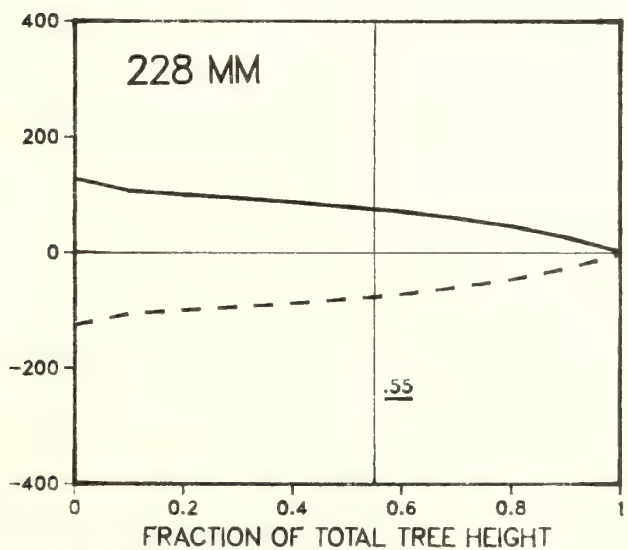
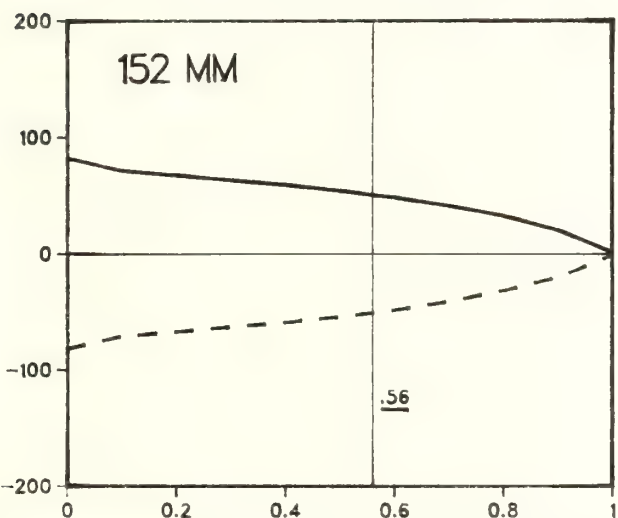
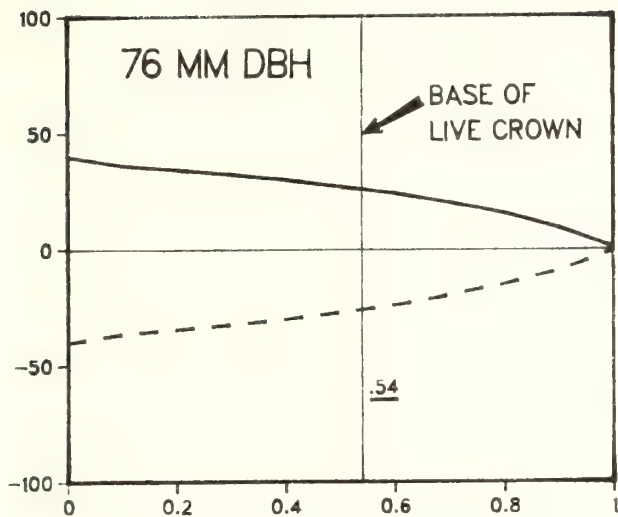


Figure 3-2—Crown base position related to stemwood form in *latifolia* trees of three diameters from low-elevation zones. The dashed lines are mirror images of the solid lines.

LATIFOLIA MEDIUM ELEVATION



LATIFOLIA HIGH ELEVATION

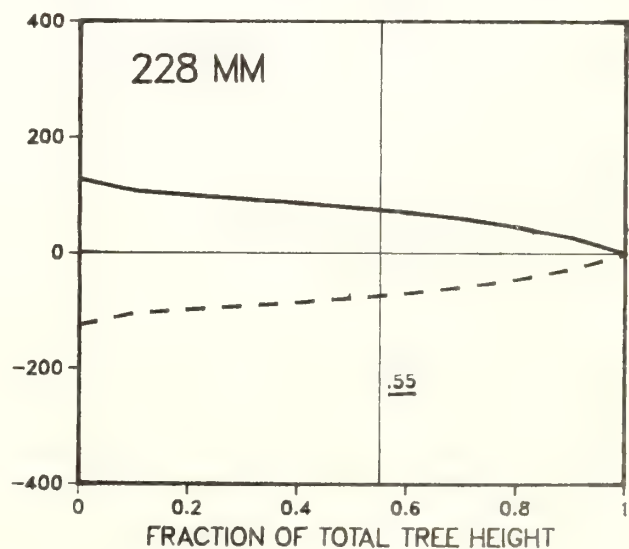
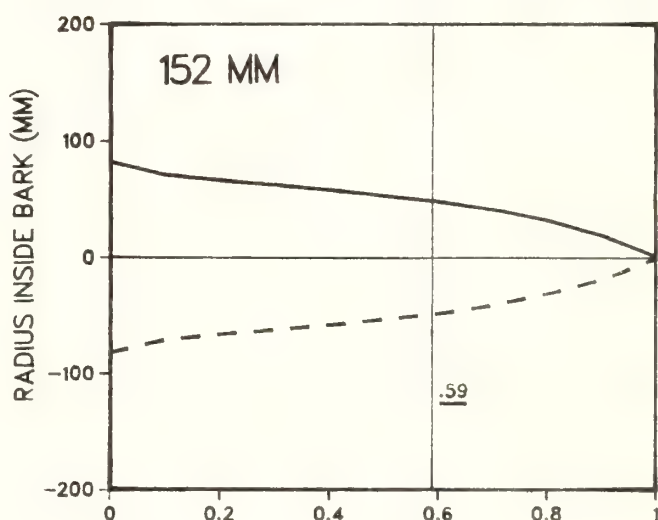
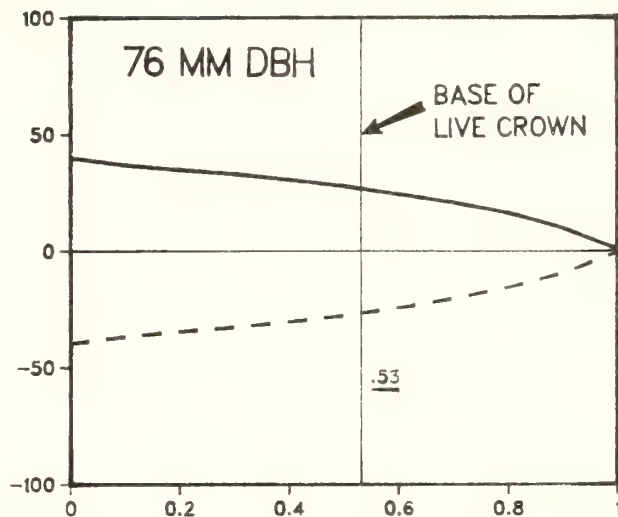


Figure 3-3—Crown base position related to stemwood form in *latifolia* trees of three diameters from medium-elevation zones. The dashed lines are mirror images of the solid lines.

Figure 3-4—Crown base position related to stemwood form in *latifolia* trees of three diameters from high-elevation zones. The dashed lines are mirror images of the solid lines.

Stems of large-diameter *latifolia* flared more at the butt than those of small diameter—both inside bark (fig. 3-5) and outside bark (fig. 3-6); in other respects, stems of the three diameters had similar forms.

Stem diameters at various levels in trees of the three diameters, inside and outside bark, are given in table 3-2. In constructing this table latitudinal and elevational data were pooled. Standard deviations were greatest at stump-top level. Trees 76 mm in d.b.h. had 25 mm diameter inside bark at a level between 0.8 and 0.9, while for the two larger diameter classes, this diameter was reached above the 0.9 level. (See also fig. 1-7.)

Table 3-2—*Latifolia* stem diameters inside and outside bark from 152-mm stump height to apical tip at 11 levels in trees of three diameters; latitudinal and elevational data pooled

Fraction of stem height above stump	Inside bark		Outside bark	
	Average	Std. deviation	Average	Std. deviation
----- Millimeters -----				
76 mm d.b.h.				
0	79.4	4.5	87.4	5.3
0.1	72.5	2.8	78.1	3.3
.2	68.8	2.7	74.0	3.0
.3	65.0	3.8	69.9	3.6
.4	60.0	3.8	64.8	4.0
.5	54.3	4.0	58.8	4.4
.6	47.7	4.7	52.1	5.0
.7	39.6	5.0	43.8	5.4
.8	30.2	5.0	34.0	5.3
.9	18.0	4.5	21.4	4.6
1.0	1.7	1.7	6.2	1.7
152 mm d.b.h.				
0	163.3	7.0	175.5	10.2
0.1	140.9	3.6	149.1	4.0
.2	132.9	4.3	140.4	4.7
.3	124.7	4.8	131.8	5.0
.4	117.2	5.4	124.1	5.8
.5	107.3	6.0	114.1	6.3
.6	96.1	6.6	102.9	6.9
.7	81.4	7.8	87.9	8.0
.8	62.8	7.7	68.7	8.0
.9	37.7	8.5	42.1	8.0
1.0	1.7	2.4	7.4	1.9
228 mm d.b.h.				
0	253.1	15.1	270.4	18.5
0.1	210.9	5.1	221.3	5.1
.2	197.7	6.8	207.4	6.9
.3	186.1	7.4	195.3	7.7
.4	173.3	8.5	182.2	8.8
.5	158.1	9.5	167.0	9.9
.6	141.1	10.6	150.3	11.2
.7	118.5	11.4	126.7	12.0
.8	89.9	10.9	97.3	11.4
.9	51.7	9.1	57.6	9.8
1.0	1.7	2.5	7.4	2.1

LATIFOLIA

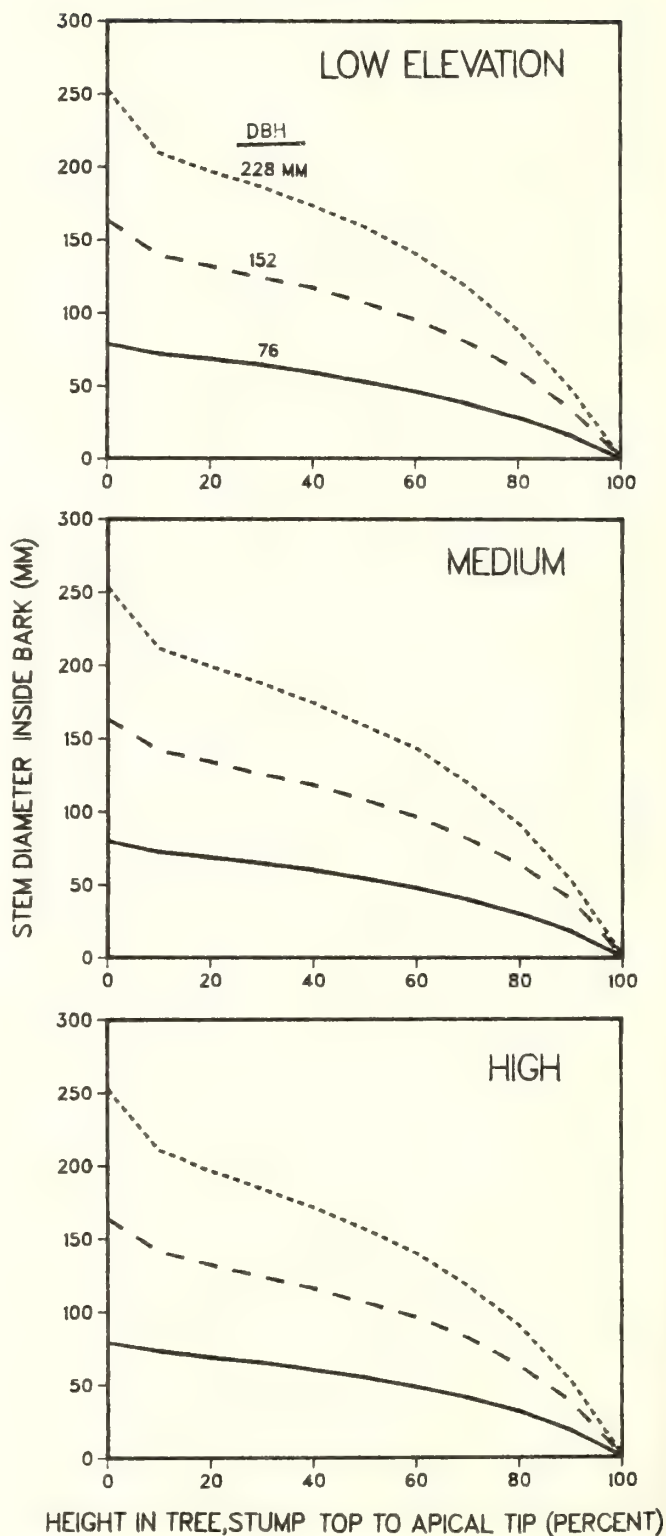


Figure 3-5—Inside bark stem diameters of *latifolia* trees 76, 152, and 228 mm in d.b.h. related to height in tree and elevational zone; latitudinal data pooled.

LATIFOLIA

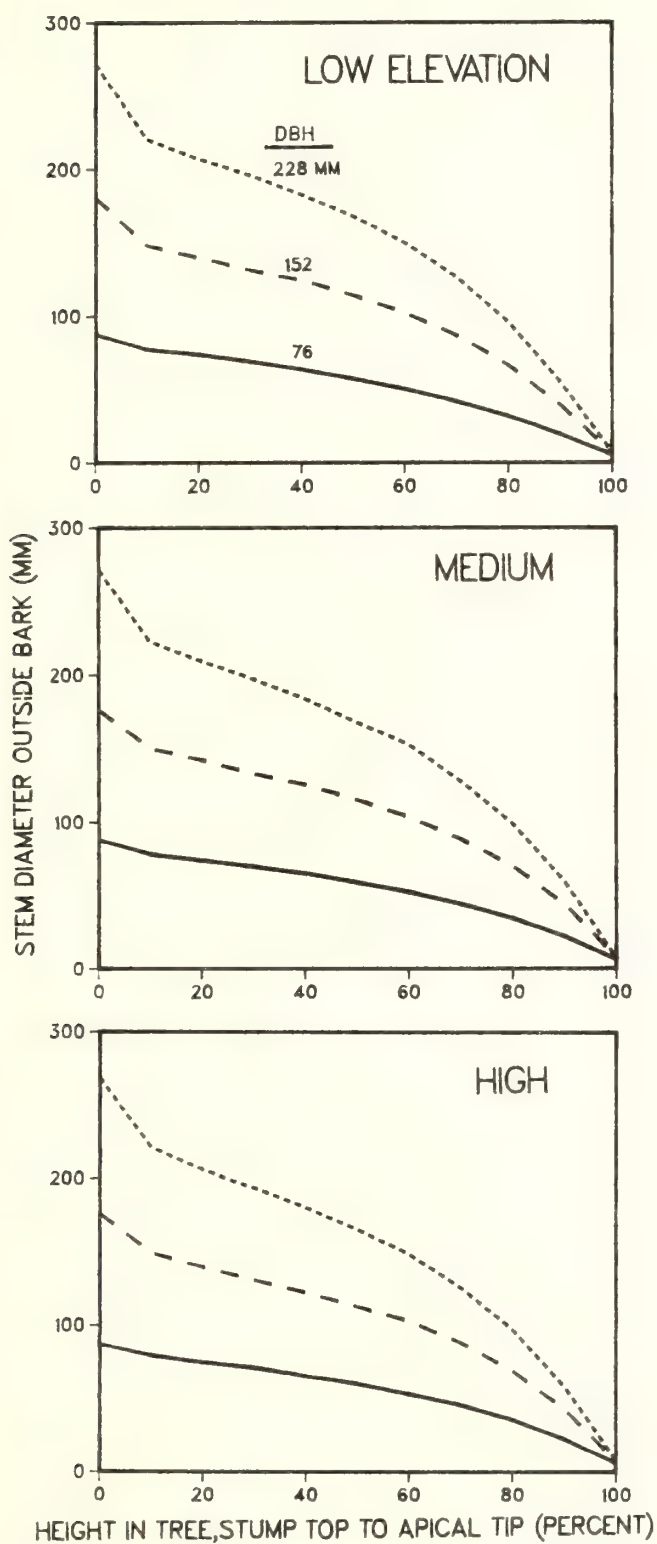


Figure 3-6—Outside bark stem diameters of *latifolia* trees 76, 152, and 228 mm in d.b.h. related to height in tree and elevational zone; latitudinal data pooled.

LATIFOLIA

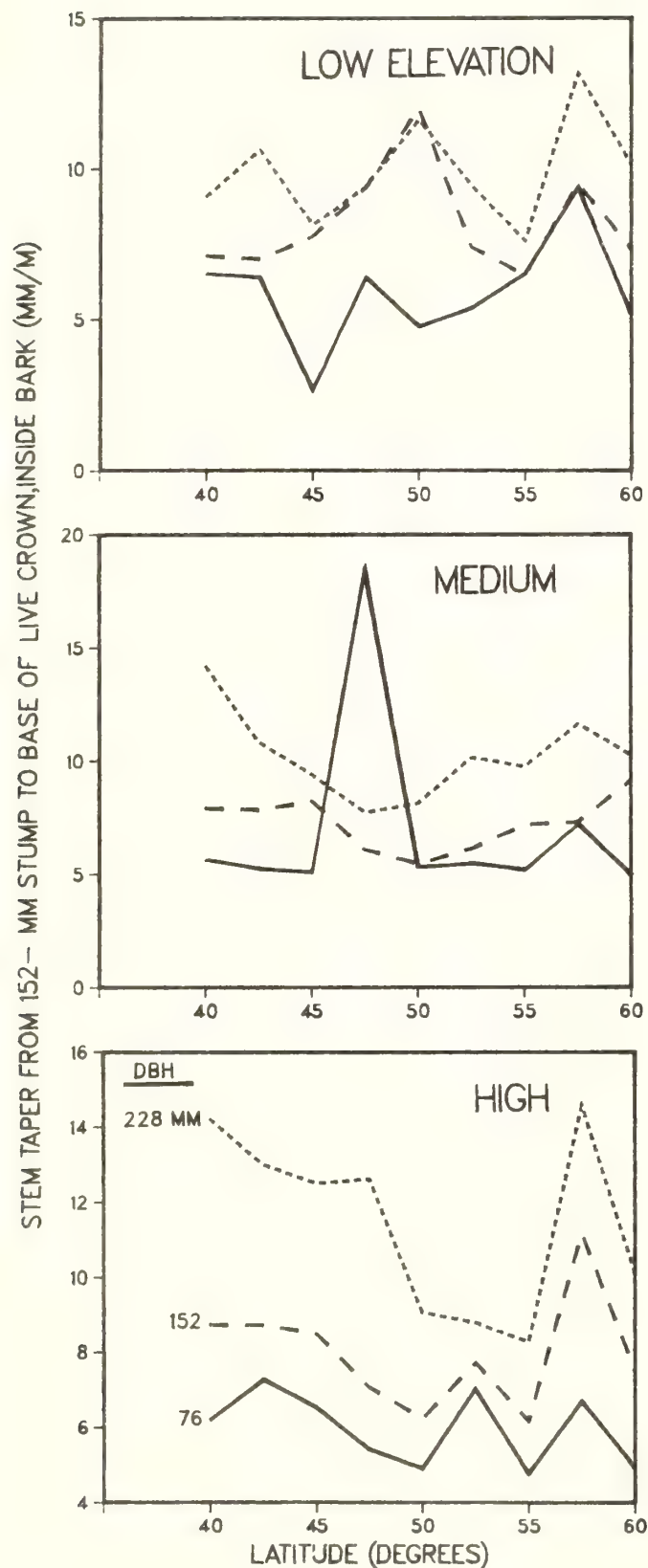


Figure 3-7—Below-crown, inside bark, average stem taper in *latifolia* trees of three diameters related to latitude and elevational zone.

Stem Taper From 152-mm Stump Height to Base of Live Crown, Inside Bark

Below-crown stem taper inside bark averaged 8.2 mm/m, with standard deviation of 3.6 mm/m. Analysis for significant differences was difficult because of unequal variances—mainly occurring with 76-mm trees at 47.5 degrees latitude—particularly at medium elevation (fig. 3-7). The data (figs. 3-7 and 3-8) show that below-crown taper is positively correlated with d.b.h. ($r = 0.487$), and that 228-mm trees from high-elevation zones tend to have more below-crown stem taper than those from low- or medium-elevation zones (fig. 3-8). By elevational zone, below-crown stemwood taper averaged as follows (diameter and latitudinal data pooled):

Elevational zone	Average	Standard deviation
----- mm/m -----		
Low	8.0	3.3
Medium	8.1	4.0
High	8.5	3.5

Below-crown stem taper inside bark for the three diameters averaged as follows:

D.b.h.	Average	Standard deviation
----- mm/m -----		
mm		
76	6.3	3.6
152	7.8	2.6
228	10.5	3.3

Latitudinal differences varied with diameter (fig. 3-7), but the averages—with elevational and diameter data pooled—all fell within the range of $8 \text{ mm/m} \pm 1 \text{ mm/m}$, except for latitudes 47.5, 55, and 57.5 degrees, where taper averaged 9.2, 6.9, and 10.1, respectively. With the exception of 57.5 degrees, trees in Canadian latitudes

LATIFOLIA

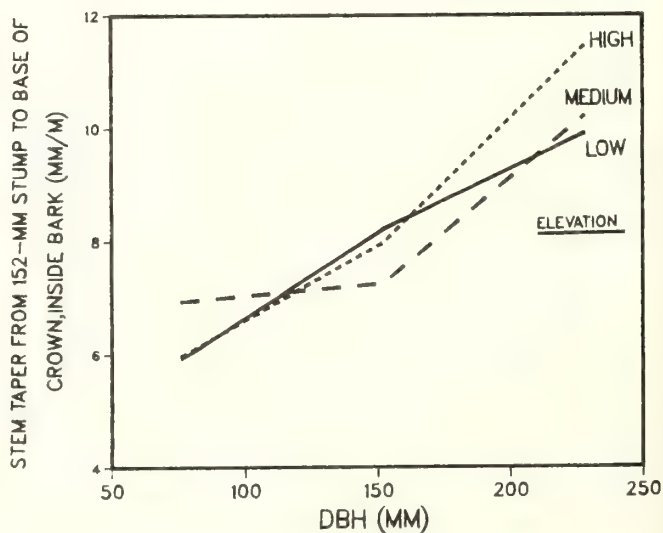


Figure 3-8—Below-crown, inside bark, average stem taper in *latifolia* trees related to d.b.h. and elevational zone; latitudinal data pooled.

averaged less than 8 mm/m; those within the United States, with the exception of 45 degrees, averaged more than 8 mm/m.

Correlations between below-crown stemwood taper and the following measured properties are of interest:

Property	<i>r</i>
Stem diameter at base of live crown, inside bark	0.554
Stem diameter at 152 mm stump height, inside bark	.521
Foliage weight, oven-dry basis	.519
Average annual ring width at stump height	.502
Volume of live branches, wood plus bark	.499
Weight of live branches, wood plus bark, oven-dry	.495
D.b.h.	.487
Crown width	.460
Average diameter of live branches	.447
Volume of complete-tree bark (stump-root, stem, branches)	.438
Weight of central stump-root system, wood plus bark, oven-dry	.431

These data indicate that below-crown stemwood tapers least in small-diameter, slow-grown trees with little foliage, small branches, narrow crowns, thin bark, and small central stump-root systems.

Stem Taper From Base of Live Crown to Apical Tip, Inside Bark

Within-crown inside bark stem taper averaged 15.8 mm/m, with standard deviation of 4.1 mm/m—nearly double that of below-crown stem taper. Within-crown stem taper was positively correlated with d.b.h. ($r = 0.535$) and with elevational zone (fig. 3-9), but these relationships were complicated by interactions with latitude (fig. 3-10).

LATIFOLIA

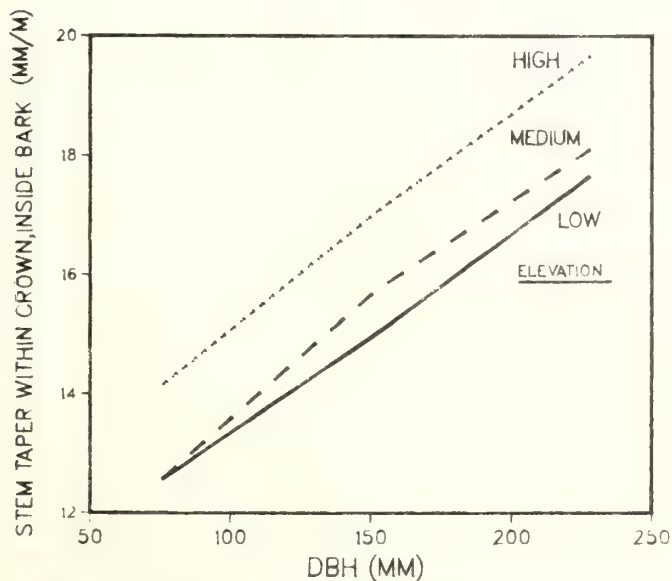


Figure 3-9—Within-crown, inside bark, average stem taper in *latifolia* trees (latitudinal data pooled) related to d.b.h. and elevational zone.

LATIFOLIA

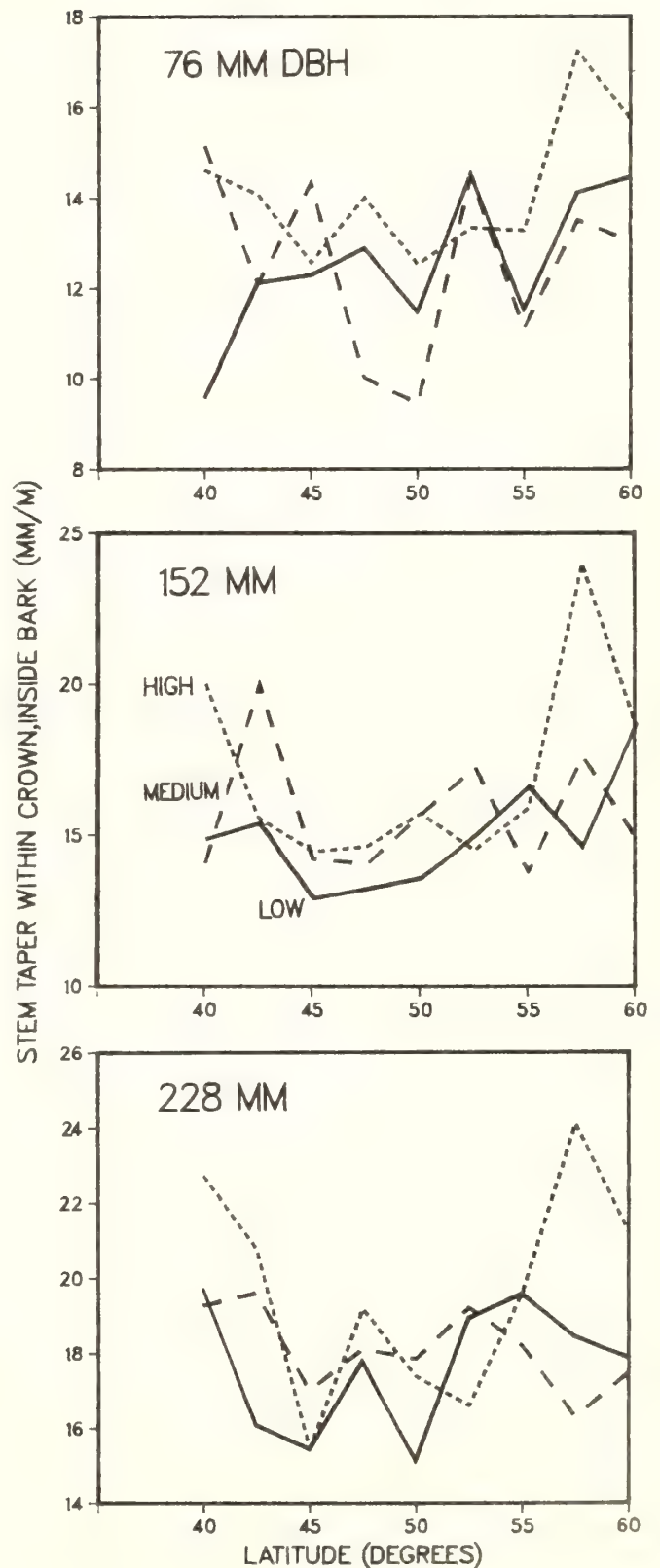


Figure 3-10—Within-crown, inside bark, average stem taper in *latifolia* trees of three diameters related to latitude and elevational zone.

Averages by diameter were as follows:

D.b.h.	Average	Standard deviation
mm	----- mm/m -----	
76	13.1	3.1
152	15.9	3.8
228	18.5	3.5

Unequal variances made analysis for significant differences difficult, but with diameter and elevational data pooled, *latifolia* trees from midlatitudes (45 through 55 degrees) had less within-crown taper than those from the southern and northern extremities of the range (fig. 3-11).

Correlations between within-crown stemwood taper and the following measured properties are of interest:

Property	r
Live branch diameter	0.595
Heartwood diameter at 152 mm stump height	.583
Stemwood diameter at 152 mm stump height	.536
D.b.h. (outside bark)	.535
Tree age at 152 mm stump height	.533
Weight of central stump-root system, wood plus bark, ovendry	.506
Volume of complete-tree bark (stump-root, stem, branch)	.477
Crown width	.466
Stem gross volume, wood plus bark	.459
Weight of stem, wood plus bark, ovendry	.457
Weight of live branches, wood plus bark, ovendry	.449
Volume of live branches, wood plus bark	.443
Crown ratio	-.443
Number of cones on the tip 305 mm of the top 25 branches	.433
Heartwood volume as percentage of stem-wood volume	.429

These data suggest that within-crown stemwood taper is least in small trees with small branches, narrow crowns with few cones, high crown ratios, low heartwood content, and small central stump-root systems.

Stem Diameter at Base of Live Crown, Inside Bark

Stem diameter inside bark at the base of the live crown was proportional to d.b.h., averaging 52 (11.4), 100 (18.5), and 148 (23.1) mm for the three diameter classes. This below-crown diameter tended to be larger in southern latitudes than northern (fig. 1-16), probably because crowns in the south were longer than in the north (figs. 1-9 and 1-17).

LATIFOLIA

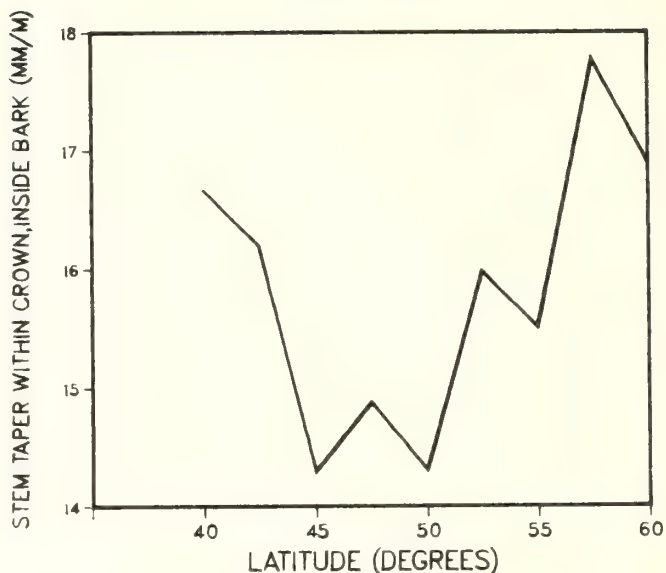


Figure 3-11—Within-crown, inside bark, average stem taper (diameter and elevational data pooled) in *latifolia* trees related to latitude.

Correlations between stemwood diameter inside bark at the base of the live crown and the following measured properties are of interest:

Property	r
D.b.h., outside bark	0.911
Diameter at 152-mm stump height, outside bark	.895
Volume of complete-tree bark	.882
Foliage weight, ovendry	.877
Weight of central stump-root system, wood plus bark, ovendry	.849
Weight of live branches, wood plus bark, ovendry	.830
Volume of live branches, wood plus bark	.830
Volume of stem, wood plus bark	.820
Weight of stem, wood plus bark, ovendry	.798
Crown length	.794
Crown width	.787
Average diameter of live branches	.752
Heartwood diameter at 152 mm stump height	.691
Sapwood thickness at 152 mm stump height	.688
Height of tree to apical tip	.675
Stembark as percentage of gross stem volume	-.631
Bark thickness at 152 mm stump height	.581

To avoid excessive taper and the expense of delimbing, users of lodgepole pine prefer that the crowns be limited to that portion of the tree stem with smaller-than-merchantable diameter. The foregoing data suggest that stem diameter inside bark at the base of the live crown is least in small, thin-barked trees with little heartwood, small stump-root systems, and short and narrow crowns with small branches.

Silviculturists note that unfortunately these characteristics typically occur where merchantable volumes per hectare are considerably below the site potential for merchantable volume production—usually because of overstocking and advanced age to reach merchantable size.

Stemwood Volume Within the Live Crown, as a Proportion of Total Stemwood Volume From 152-mm Stump Height to Apical Tip

Stemwood volume within the live crown, as a proportion of total stemwood volume, averaged 16.0 percent, with standard deviation of 12.1 percentage points. It was unrelated to elevational zone but was significantly related to latitude. Canadian latitudes averaged 12.2 percent for 50 through 60 degrees—considerably less than in U.S. latitudes where the average was 20.8 percent for 40 through 47.5 degrees (fig. 3-12).

Percentages did not differ significantly (0.05 level) by diameter; averages were as follows:

D.b.h.	Average	Standard deviation
mm	Percent	
76	17.8	13.2
152	15.6	13.0
228	14.7	9.5

Correlations between within-crown stemwood proportion of total stemwood volume and the following measured properties are of interest:

Property	r
Crown ratio	0.861
Crown length	.553
Percentage moisture content of complete tree	.548
Heartwood volume as proportion of stemwood volume	-.543
Stembark specific gravity	.407
Within-crown taper	-.382
Complete-tree specific gravity	-.352
Age of tree at 152-mm stump height	-.344
Heartwood diameter at stump height	-.318
Sapwood specific gravity	-.318
Tree height to apical tip	-.305
Stembark volume as percentage of gross stem volume	.300

These data suggest that within-crown stemwood has the least proportion of total stemwood volume in tall but short-crowned older trees having low moisture content, high heartwood content, high specific gravity of bark and sapwood, and thin stembark.

LATIFOLIA

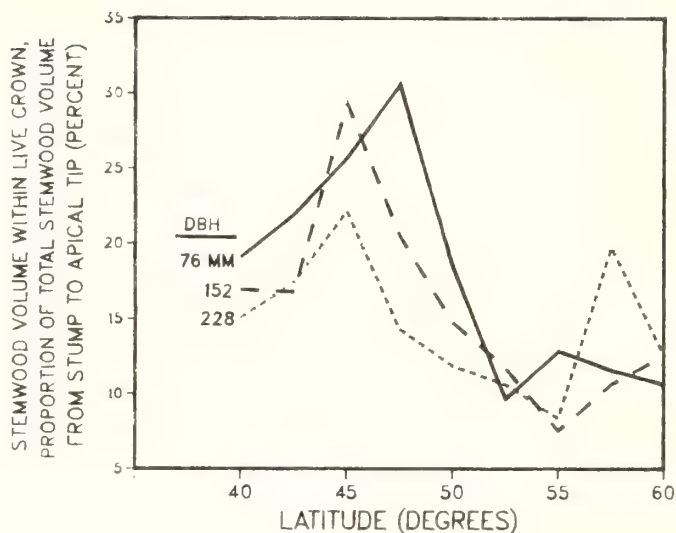


Figure 3-12—Stemwood volume in crown as a percentage of total stemwood volume in *latifolia* trees related to d.b.h. and latitude.

MURRAYANA

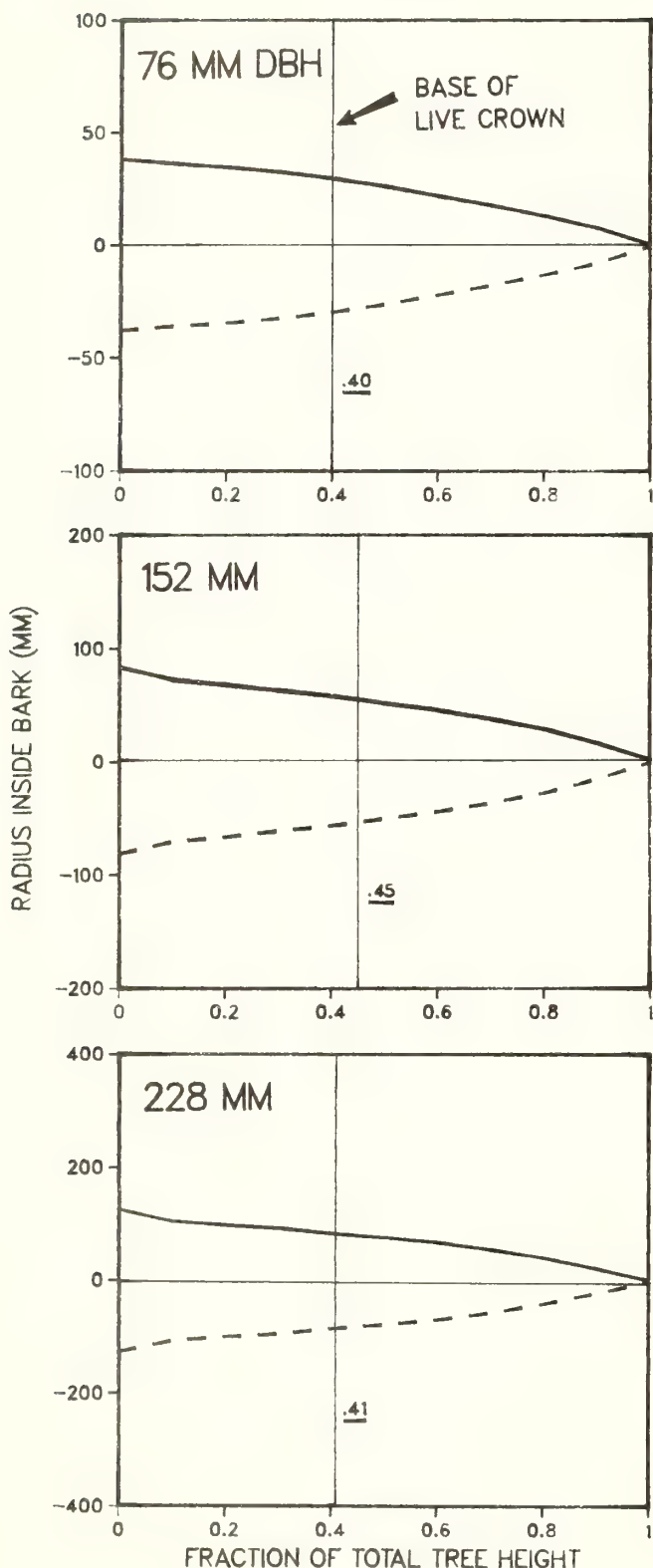


Figure 3-13—Crown base position related to stemwood form of *murrayana* trees of three diameters. The dashed lines are mirror images of the solid lines.

3-6 RESULTS—MURRAYANA

Because the entire *murrayana* sample totaled but 36 trees, correlations among tree characteristics are not noted in the detail provided for the 243 *latifolia* trees. Standard deviations for diameter-class data are noted in parentheses following their average values, as they were in the *latifolia* results section.

Even with this small sample (nine trees per latitude), some latitudinal differences were observed. Only those statistically significant (5-percent level) are graphed or tabulated.

Stem Form

As with *latifolia*, *murrayana* stem form, inside bark, is comprised of three geometric shapes; the section within the crown has significantly greater taper than that below the crown (fig. 3-13). Trees 76 mm in d.b.h. have little butt flare in the first 10 percent of tree height, but this flare becomes distinct in trees 152 and 228 mm in d.b.h. (figs. 3-13 and 3-14).

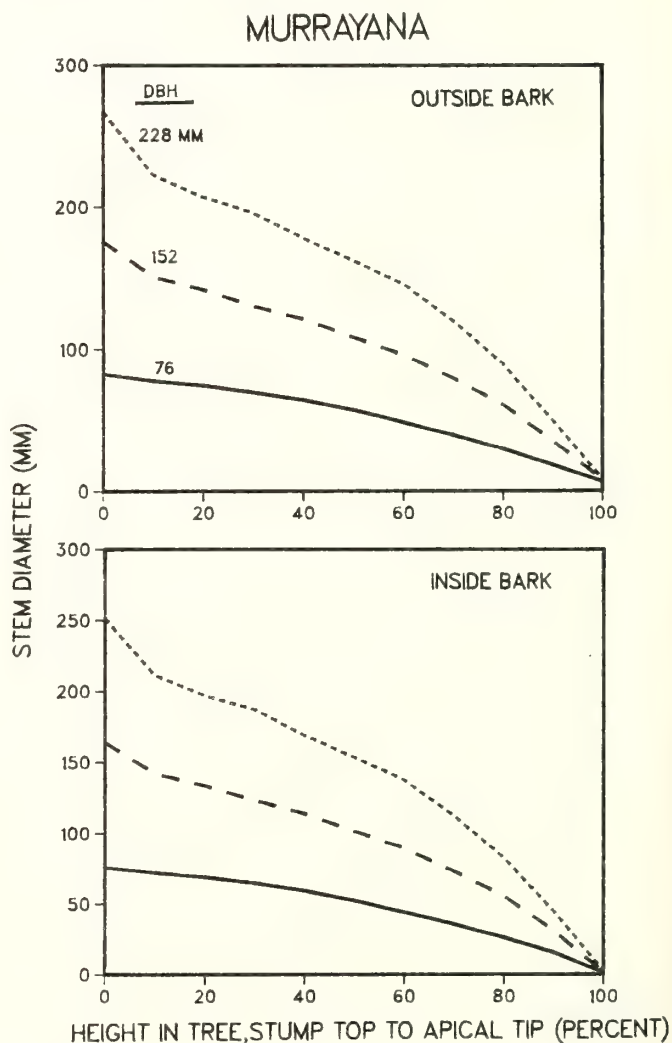


Figure 3-14—Outside bark and inside bark stem diameters of *murrayana* trees 76, 152, and 228 mm in d.b.h. related to height in tree; latitudinal data pooled.

Stem diameters at 10 percent height intervals in trees of the three diameters, inside and outside bark, are given in table 3-3. In constructing this table, latitudinal data were pooled. Standard deviations were generally greatest at stump top and at about 80 percent of tree height. Trees 76 mm in d.b.h. had a 25-mm top diameter inside bark at the 0.8 level; for 152- and 228-mm trees, however, this top diameter fell above the 0.9 level. (See also fig. 1-56.)

Table 3-3—*Murrayana* stem diameters inside and outside bark from 152-mm stump height to apical tip at 11 levels in trees of three diameters; latitudinal and elevational data pooled

Fraction of stem height above stump	Inside bark		Outside bark	
	Average	Std. deviation	Average	Std. deviation
----- Millimeters -----				
76 mm d.b.h.				
0	75.8	6.4	82.5	7.1
0.1	72.8	4.1	77.7	4.9
.2	69.0	3.1	74.4	3.4
.3	64.8	3.6	69.6	4.3
.4	59.2	3.8	64.2	4.9
.5	52.3	3.6	57.0	4.4
.6	44.0	3.2	48.3	3.6
.7	35.4	2.8	39.3	2.9
.8	25.9	3.1	29.5	3.0
.9	15.5	3.0	18.4	3.2
1.0	1.1	1.6	6.6	1.4
152 mm d.b.h.				
0	163.9	9.2	175.7	9.5
0.1	142.0	2.9	151.0	3.4
.2	133.5	4.7	141.8	5.0
.3	123.1	5.0	130.5	4.9
.4	113.8	6.6	121.3	6.2
.5	101.3	7.8	108.5	7.5
.6	89.1	9.6	95.9	9.5
.7	72.9	11.4	79.5	11.5
.8	55.4	11.3	60.8	11.6
.9	30.6	8.7	35.1	8.9
1.0	1.6	2.4	8.0	1.4
228 mm d.b.h.				
0	251.3	13.9	266.8	15.1
0.1	211.3	5.9	222.7	6.6
.2	196.9	8.7	206.8	10.2
.3	186.8	9.2	196.0	9.8
.4	168.9	7.6	178.2	8.1
.5	153.3	8.2	162.3	8.9
.6	137.3	7.6	145.7	8.1
.7	112.2	12.6	119.8	12.8
.8	82.2	12.0	89.3	11.9
.9	44.4	12.0	49.5	12.1
1.0	2.3	3.0	8.4	2.0

Stem Taper From 152-mm Stump Height to Base of Live Crown, Inside Bark

Stemwood taper from stump top to base of live crown averaged 9.5 mm/m, with standard deviation of 4.7 mm/m. Trees in the two northern latitudes had less below-crown stemwood taper than those from the two southern latitudes (fig. 3-15). Small trees averaged less below-crown stemwood taper than large trees, as follows (see also fig. 3-15):

D.b.h.	Average	Standard deviation
mm	mm/m	
76	5.8	2.3
152	10.8	5.1
228	11.9	4.2

Stem Taper From Base of Live Crown to Apical Tip, Inside Bark

Within-crown stemwood taper was two-thirds larger than below-crown taper. It averaged 15.7 mm/m, with standard deviation of 4.8 mm/m, and was unrelated to either d.b.h. or latitude.

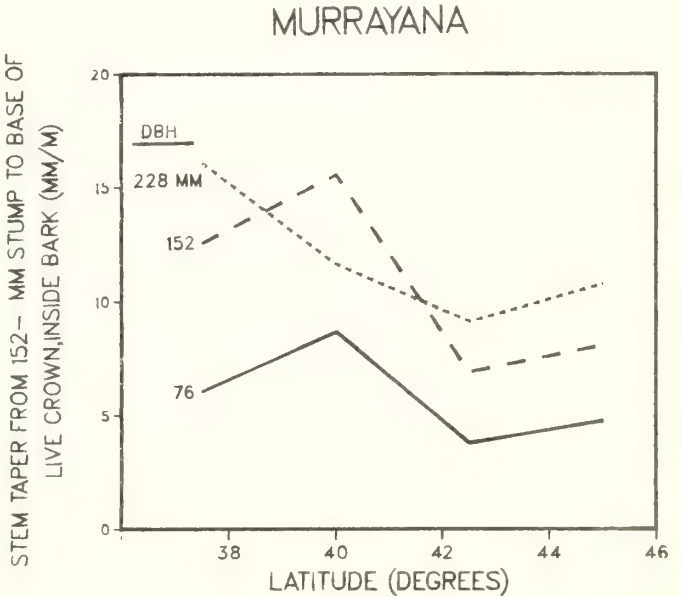


Figure 3-15—Below-crown, inside bark, average stem taper in *murrayana* trees of three diameters related to latitude.

Stem Diameter at Base of Live Crown, Inside Bark

Stem diameter at the base of the live crown was not significantly related to latitude, but was positively correlated with d.b.h., averaging 58 (12), 108 (17), and 169 (21) mm for the three diameter classes.

Stemwood Volume Within Live Crown, as a Proportion of Total Stemwood Volume From 152-mm Stump Height to Apical Tip

Stemwood volume within the live crown, as a percentage of total stemwood volume, averaged 26.5 percent, with standard deviation of 13.8 percentage points. It was unrelated to d.b.h., but trees in the two southern latitudes had a greater percentage of crown stemwood than those in the two northern latitudes, as follows:

Latitude	Average	Standard
Degrees	Percent	deviation
37.5	33.9	12.7
40	28.3	17.8
42.5	20.4	11.9
45	23.4	9.7

3-7 RESULTS—LATIFOLIA COMPARED TO MURRAYANA

The experimental design permitted an orthogonal comparison between the two varieties at three latitudes as follows:

Varieties:	(2)	<i>latifolia</i> and <i>murrayana</i>
D.b.h. classes:	(3)	76, 152, and 228 mm
Latitudinal zones:	(3)	40, 42.5, and 45 degrees
Elevational zones:	(1)	medium (1,148 m to 2,711 m)
Replications:	(3)	

Sample size for this comparison therefore totaled 54 trees, 27 of each variety. In the discussion that follows, only significant relationships associated with varietal differences are explained; the other effects are more completely described in the preceding two results sections. No statistically significant varietal differences were observed in within-crown stem taper, diameter inside bark at the base of the live crown, or percentage of total stemwood volume found in the live crown. At 42.5 degrees latitude in all three diameters, *latifolia* had more below-crown stemwood taper than *murrayana*; at 45 degrees, the *latifolia* trees of 76 and 152 mm d.b.h. also had more below-crown taper than *murrayana*. In trees 76 and 152 mm in d.b.h. at 40 degrees, however, *murrayana* had more below-crown stemwood taper than *latifolia* (fig. 3-16).

COMPARISON

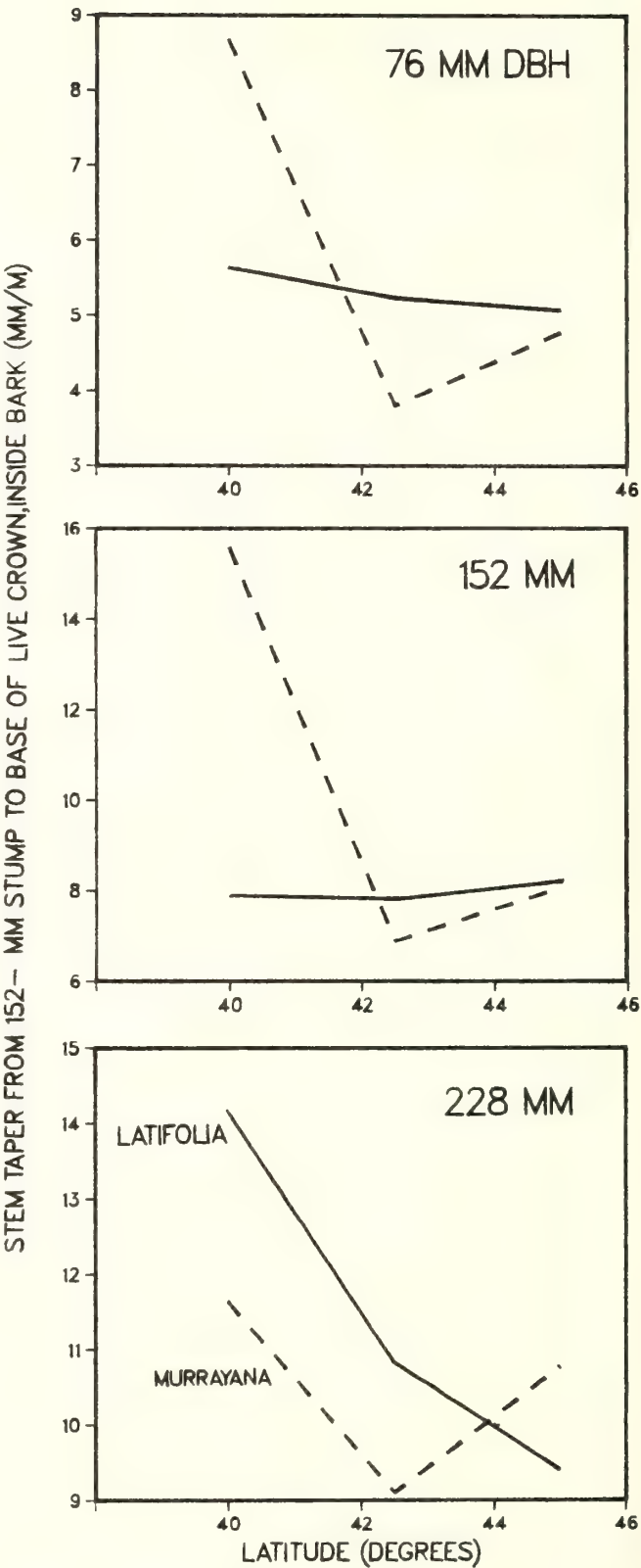


Figure 3-16—Below-crown, inside bark, average stem taper of *latifolia* trees compared to *murrayana* related to latitude.

CHAPTER 4: SPECIFIC GRAVITIES AND WEIGHTS OF TREE COMPONENTS

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4-1 INTRODUCTION

Statistical information on weight of tree components when green is needed to plan harvesting activities and green-wood transport. Oven-dry weights are needed to develop process material balances in wood conversion plants.

Specific gravity, a unitless measure of density relating wood or bark weight to the weight of water, is a simple and useful index to the suitability of wood and bark for many important uses. It is closely correlated with the mechanical properties of wood and is therefore a primary factor in the segregation of wood for high-strength lumber, posts, poles, and cross-ties. Density, frequently expressed as specific gravity, largely determines pulp yield from a given volume of wood; that is, a cord of high-density lodgepole pine will yield significantly more pounds of pulp than an equal volume of low-density wood of the same species. Similarly, a cord of high-density wood and bark will yield more heat when burned for energy than a cord of low-density wood.

4-2 OBJECTIVE AND SCOPE

Only those weight and specific gravity parameters most important to processors of lodgepole pine are discussed in this chapter. No attempt is made to construct equations predicting weights, and only two specific gravity prediction equations are developed—one for wood and one for bark based on average growth-ring width at 152-mm stump height. Graphs are presented of data aggregated in various significant ways, however, that permit reading of weight and specific gravity information directly from observed study data.

As previously noted, the characterization effort is confined to two varieties of lodgepole pine: *Pinus contorta* var. *latifolia* Engelm. and *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm., with emphasis on the former. The primary objective during tree collection was to obtain three replications of disease- and insect-free specimens of var. *latifolia* measuring 76, 152, and 228 mm in diameter at breast height (d.b.h.) at low, medium, and high elevations from nine equally spaced north latitudinal zones (40 to 60 degrees) across 10 degrees of longitude in such a way as to encompass the major range of this variety (fig. 1-1).

A secondary objective was to sample three replications of these same three diameter classes of var. *murrayana* at midelevation at four north latitudes (37.5, 40, 42.5, and 45 degrees) in California and Oregon at a single longitude per latitude (fig. 1-1).

The trees of both varieties were sampled in such a way that between-variety comparisons could be made for mid-elevation trees at latitudes 40, 42.5, and 45 degrees. The sampling plan does not permit computation of species-average values. The collection totaled 243 *latifolia* and 36 *murrayana* trees.

Explanations of statistical analyses procedures and a table of analyses of variance formats, with degrees of freedom indicated, are shown in table 1-2. In the results portion of this report standard deviations are noted in the text in parentheses following average values. Correlations of interest observed in *latifolia* between component

weights (and specific gravities) and tree characteristics are also noted in the results section of this chapter.

4-3 LITERATURE REVIEW

There is a substantial body of literature on the weight of lodgepole pine components—much of it related to fire research, and a smaller literature related to specific gravity of tree components. Following is an abstract of this information, with emphasis on North American data.

Weight of Tree Components

Complete Trees—Adamovich (1975) sampled lodgepole pine from good sites about 70 miles north of Prince George, BC, to determine aboveground tree component proportions and green weights. Proportions determined were as follows:

Component	Proportion of green weight and standard deviation	
	----- Percent -----	
Stemwood	86.8	(1.43)
Stembark	6.6	(.83)
Branches with foliage	6.6	(1.52)
Total	100.0	

His equation ($R^2 = 0.992$) for green whole-tree weight, including all aboveground portions, follows (logarithmic, base 10):

$$\log \text{ of whole-tree weight, pounds} = -0.946 + 1.608 \log D + 1.257 \log H$$

where:

D = d.b.h., inches

H = tree height, feet.

In Crater Lake National Park, Agee (1983) sampled understory *murrayana* of small diameter (0.86 to 5.88 cm groundline diameter). He found that aboveground tree biomass, oven-dry-weight basis, was best expressed as a natural logarithmic function of tree height, as follows:

$$\text{in dense stands } (R^2 = 0.95)$$

$$\ln Y = -1.0415 + 2.4574 \ln X$$

$$\text{in open stands } (R^2 = 0.96)$$

$$\ln Y = -0.2727 + 2.4567 \ln X$$

where:

Y = aboveground biomass per tree, grams

X = tree height from ground to apical tip, meters.

Chapman and others (1982) sampled trees 12 inches in d.b.h. and smaller in northeastern Washington (Stevens, Ferry, and Pend Oreille Counties). They found that total aboveground weight, green basis, could be predicted ($R^2 = 0.90$) as follows:

$$Y = 5.540 + 13.2964D^2H$$

where:

Y = total aboveground biomass green weight, pounds

D = d.b.h., inches

H = tree height, feet.

Johnstone (1971) studied three stands of 100-year-old trees in southwestern Alberta and observed the following average proportions for tree components (ovendry-weight basis) (two of the stands averaged 7.1 inches d.b.h., and the third was only 2.2 inches):

Component	7.1-inch	2.2-inch
	stands	stand
	----- Percent -----	
Needles	5	7
Branches	7	13
Stem, wood plus bark	73	61
Root plus stump	15	19
Total	100	100

His equations (logarithmic to the base 10) for tree component weights follow and are based on data pooled from two of the three stands in which d.b.h. averaged 7.1 inches, height 60.4 feet, and crown length 21.6 feet; *D* = d.b.h., inches; *H* = tree height, feet:

log dry needle weight, pounds = -0.996 + 1.148 log *D*²*H*

log dry branch weight, pounds = -4.126 + 1.509 log *D*²*H*

log dry stem weight, wood plus bark, pounds =
-0.889 + 0.938 log *D*²*H*

log dry stump-root weight, pounds = -1.879 + 1.022 log *D*²*H*

log dry complete-tree weight, pounds =
-0.996 + 0.997 log *D*²*H*

*R*² values for the foregoing equations were 0.849, 0.894, 0.978, 0.949, and 0.987, respectively. The equations were based on 72 or 85 trees.

Pearson (1982) found from a study in the Medicine Bow Mountains of southeastern Wyoming that trees grown in very open stands (<1,000 trees/ha) had 28 percent more biomass than trees of the same diameter in very dense stands (>5,000 stems/ha). Biomass of foliage, branches, boles, and woody lateral roots of individual trees decreased by 73, 25, 25, and 80 percent, respectively, across this density gradient, but root crown biomass increased by 25 percent. Sapwood area was a more precise predictor of foliage biomass than basal area, except in very dense stands. For stands of various densities, the biomass distribution varied as follows:

Component	Stand density (trees/ha)			
	<1,000	1,000-1,500	1,500-5,000	>5,000
Percent of complete-tree weight, ovendry				
Foliage	13	12	7	5
Branches	8	8	8	8
Bole, wood plus bark	61	63	60	62
Root crown	13	14	22	23
Lateral roots	5	3	3	2

Based on a sample of 60 trees from Alberta, Canada, Singh (1982b) tabulated aboveground weights, ovendry basis and foliage-free, of lodgepole pine related to d.b.h. and height; his table is abstracted as follows:

D.b.h.	Tree height, meters					
	8	12	16	20	24	28
<i>cm</i>	----- Kilograms -----					
8	8	19				
12	26	38	51			
16		61	80	99		
20		89	116	143	169	
24			160	196	232	269
28			212	260	308	356
32				336	397	459

Based on the same sample of 60 trees, Singh (1982a) gives equations for predicting ovendry weights of stump, stem, and live branches—all based on d.b.h. and height.

From the literature, Smith and DeBell (1973) estimated biomass distribution (ovendry basis) in aboveground portions of lodgepole pine, as follows: stemwood, 65 percent; stembark, 10 percent; branches, 16 percent; and foliage, 9 percent.

Weaver and Forcella (1977), from reviews of the literature and data from a 39-tree sample in Montana, concluded that functions of the logarithm (base 10) of *D*²*H* are good predictors of logarithms of lodgepole pine component weight. They noted that predictions of weight from such relationships become poorer for environments increasingly different from those for which the relationships were developed.

Foliage—In Crater Lake National Park, Agee (1983) sampled understory *murrayana* of small diameter (0.86 to 5.88 cm groundline diameter). He found that foliage weight, ovendry, was best expressed as a natural logarithmic function of diameter, as follows:

in dense stands (*R*² = 0.70)

ln *Y* = -1.1430 + 1.5001 ln *X*

in open stands (*R*² = 0.95)

ln *Y* = -1.8756 + 1.9529 ln *X*

where:

Y = foliar biomass dry weight, grams

X = groundline diameter, centimeters.

Brown (1978) found that in lodgepole pines 1-inch d.b.h. or less, foliage averages about 52 percent of the weight of live branches including foliage, ovendry basis; for larger trees the decimal fraction represented by foliage equals 0.493 - 0.0117 (d.b.h), with d.b.h. expressed in inches.

Dobie and McIntosh (1976) found that foliage on 8-inch d.b.h. whole lodgepole pine trees summer-harvested in Alberta averaged only 2.4 percent of their ovendry weight as delivered to a mill. The proportion was small because some trees had broken tops and others no foliage at time of mill delivery.

Based on 12 lodgepole pines 10 to 60 years old destructively sampled in the Central Colorado Mountains at an elevation of 2,700 m, Running (1980) developed the following equation for predicting foliage ovendry weight from sapwood basal area at breast height (*R*² = 0.94):

Y = -0.76 + 0.051 *X*

where:

Y = foliage ovendry weight, kilograms

X = sapwood basal area, square centimeters.

Kaufmann and Troendle (1981) also found that ovendry foliage weight of lodgepole pine is linearly related to sapwood cross-sectional area at breast height in the stem, as follows ($R^2 = 0.95$):

$$\text{Dry foliage weight, grams} = 46.2 (\text{sapwood cross-sectional area, cm}^2)$$

This equation is based on 11 trees sampled in August and September at about 915 m elevation near Fraser, CO.

Moir and Francis (1972) measured the foliage weight of 15 trees 3.6 to 19.3 cm d.b.h. sampled from three stands in the Colorado Front Range, partitioned into current year's foliage and previous year's foliage; because it is information peripheral to this paper, their results are not abstracted.

Moore (1981), in a study of lodgepole pine from Colorado, Wyoming, and Montana, found that the average weight of a fascicle of needles (ovendry basis) was 3.5 mg, with range from 2.0 to 6.1 mg; strong latitudinal or elevational trends in fascicle weight were not found.

Cones—In a survey including lodgepole pine from Colorado, Wyoming, and Montana, Moore (1981) found that ovendry weights of individual cones varied significantly with location, but not in an easily identified latitudinal or longitudinal pattern; mean weights for the 13 areas studied varied from 3.82 to 7.18 g per cone. The overall average ovendry weight per cone was 5.6 g.

Branches—Adamovich (1975) developed the following equation for green branch weights, including wood, bark, and foliage ($R^2 = 0.951$); the equation is based on trees sampled about 70 miles north of Prince George, BC:

$$\log (\text{base } 10) \text{ green branch weight, pounds} = -2.53 + 2.272 \log D + 0.553 \log (L/H)$$

where:

D = d.b.h., inches

H = tree height, feet

L = crown length, feet.

Brown and others (1977) developed predictive relationships between slash weight and tree d.b.h. from trees sampled in Montana and Idaho, expressed as weight per tree of crowns (including foliage) and nonmerchantable stem tips to various stem top diameters, as follows:

D.b.h. Inches	Crown above a		
	3-inch top	4-inch top	6-inch top
4	29		
6	46	62	
8	74	86	158
10	112	122	177
12	155	164	207
14	205	213	249
16	262	269	299

- - - Pounds, ovendry basis - - -

Brown (1978) developed an equation ($R^2 = 0.88$) to predict live branch weight of lodgepole larger than 1-inch d.b.h., as follows (ovendry basis):

$$\text{branch weight with foliage, pounds} = 0.02238 D^3 + 0.1233 D^2 R - 2.00$$

where:

D = d.b.h., inches

R = crown ratio.

He concluded that the dead-branch weight (ovendry) was as follows:

for trees 10 inches or less in d.b.h.

$$\text{weight, pounds} = 0.026D - 0.025 (\text{live branch weight})$$

for trees larger than 10 inches d.b.h.

$$\text{weight, pounds} = 0.235 (\text{live branch weight})$$

Snell and Brown (1980) estimated the ovendry weight of entire crowns (wood plus bark and foliage) above that portion of the stem that has a top diameter of 6 inches outside bark, as follows:

D.b.h. Inches	Ovendry weight Pounds
8	177
10	201
12	224
14	258
16	301

Stems—Adamovich (1975) developed the following equations for green stem weights, wood plus bark ($R^2 = 0.993$), and wood only ($R^2 = 0.994$); the equations are based on trees sampled about 70 miles north of Prince George, BC:

$$\log (\text{base } 10) \text{ stem weight, wood plus bark, pounds} = -1.259 + 1.507 \log D + 1.453 \log H$$

$$\log (\text{base } 10) \text{ stemwood weight, pounds} = -1.374 + 1.534 \log D + 1.487 \log H$$

where:

D = d.b.h., inches

H = tree height, feet.

From lodgepole 4 inches in d.b.h. and less in the Rocky Mountain region of the United States, Brown (1978) developed the following equation for estimating bole weights, wood plus bark, ovendry basis ($R^2 = 0.97$):

$$\text{bole weight, pounds} = 1.49 - 2.388D + 2.297D^2$$

where:

D = d.b.h., inches.

Chapman and others (1982) sampled trees 12 inches d.b.h. and smaller in northeastern Washington and found that entire green stem weights, wood plus bark, above 0.34-foot stump height could be predicted ($R^2 = 0.89$), as follows:

$$\text{stem weight, pounds} = 4.17605 + 0.14225D^2H$$

where:

D = d.b.h., inches

H = tree height, feet.

Bark—Adamovich (1975) developed the following equation for the green weight of stembark ($R^2 = 0.974$); the equation is based on trees sampled about 70 miles north of Prince George, BC:

$$\log (\text{base } 10) \text{ of stembark weight, pounds } = 0.841 + 1.877 \log D + 0.410 \log H$$

where:
D = d.b.h., inches
H = tree height, feet.

Snell and Max (1982) analyzed data from Oregon, Washington, and Idaho, and concluded that lodgepole logging residue sufficient to yield 100 kg of bark-free wood will also yield 8 kg of bark—ovendry-weight basis.

Sapwood and Heartwood—No data on the weight per tree of sapwood and heartwood were found in the literature.

Stump-Root System—See abstracts of Johnstone (1971) and Pearson (1982) previously discussed under the paragraph heading “Complete Trees.”
 Further to these previous comments, Moir (1972) estimated that the biomass of lodgepole roots larger than 5 mm in diameter constitutes about 25 percent of complete-tree biomass, ovendry basis. When reading the results section of this paper, readers should be aware that workers carefully excavating the full extent of the root system will recover a much greater weight of roots than workers who pull the central root mass—taproot with laterals intact to a radius of only 305 mm from tree pith—as was the procedure for the work reported here.

Specific Gravity and Bulk Density of Tree Components

Stemwood Bulk Density—According to the American Lumberman (1910), seasoned wood of lodgepole pine weighs 25.53 lb/ft³. Bramhall and Wellwood (1976) reported the average specific gravity of Canadian lodgepole pine lumber as 0.408 based on ovendry weight and green volume, and further noted that the average ovendry weight of a cubic foot of such green wood is 25.50 lb. Brown and others (1977), in predicting weight of upper stem portions of lodgepole pine in the western part of the United States, used bulk densities of 25.6 lb/ft³ of wood (based on the ovendry weight of a cubic foot of wood at 12 percent moisture content) and 26.5 lb/ft³ of bark (based on the ovendry weight of a cubic foot of green in-place bark). In his studies of dead lodgepole pine in the Intermountain West of the United States, Fahey (1980, 1981) used a bulk density for wood and stembark of 24 lb/ft³, ovendry, of green material. In a major study of the specific gravity of lodgepole pine in the United States, Maeglin and Wahlgren (1972) concluded that the average bulk density of lodgepole pine stemwood in trees larger than 5 inches d.b.h. in the western part of the United States (*murrayana* as well as *latifolia*) was 23.7 lb/ft³, ovendry, of green wood; data by State are shown in table 4-1.

Stemwood Tree Average Specific Gravity—Brazier (1980), reporting on the properties of lodgepole pine grown in Britain, found that average stemwood specific

Table 4-1—Bulk density and specific gravity of lodgepole pine stemwood based on ovendry weight and green volumes (Maeglin and Wahlgren 1972)¹

State	Density	Specific gravity		Standard error
		Average	Range	
	<i>Lb/ft³</i>			
California				
(1)	25.03	0.401	0.292 - 0.505	0.0088
(2)	23.29	.373	.328 - .430	.0047
Colorado	21.66	.347	.264 - .401	.0048
Idaho				
(north)	23.91	.383	.303 - .512	.0045
(south)	23.54	.377	.285 - .498	.0022
Montana				
(west)	24.22	.388	.305 - .509	.0019
(east)	22.66	.363	.319 - .405	.0051
Oregon				
(west)	26.34	.422	.328 - .554	.0137
(east)	24.10	.386	.319 - .493	.0026
Utah	22.79	.365	.284 - .425	.0025
Washington				
(west)	26.97	.432	.388 - .512	.0393
(east)	24.28	.389	.319 - .499	.0040
Wyoming	23.16	.371	.298 - .482	.0023

¹Computed from data taken from breast-height increment cores.

gravity (based on ovendry weight and green volume) was 0.375, but that trees from seed sources in the Prince George, BC, area had significantly lower stemwood specific gravity than those from seed sources of the south-coastal region of British Columbia.
 Cannell and others (1983), reporting on studies of plantations in Scotland, found that mean stemwood specific gravity at age 8 years differed by 21 percent among lodgepole pine clones originating in Alaska and British Columbia, and that there was a 22 percent drop in specific gravity between the innermost and outermost annual rings of the 8-year-old trees. For all clones, stemwood specific gravity decreased as a linear function of the logarithm (base *e*) of the annual stemwood volume production; that is, fast-grown wood had lower density than slow-grown wood. In Finland, Bjorklund (1982) also concluded that stemwood specific gravity in lodgepole pine is inversely correlated with growth-ring width; moreover, he noted that specific gravity of small lodgepole pine removed in thinnings was greater than that of sawtimber trees left to grow. Sylvander and Smith (1973) reported a similar trend for lodgepole stemwood in interior British Columbia.
 Carlson and Nimlos (1966) found that stemwood increment cores taken at breast height from lodgepole pine in Montana’s Clark Fork Valley west of Thompson Falls had higher specific gravity (0.409) than those found by Tackle (1962) in Wyoming and southern Idaho (0.386).
 In a study of lodgepole pine, ponderosa pine, and Douglas-fir from the west slope of the Sierra Nevada in California, Echols (1973) found that stemwood of lodgepole pine (*murrayana*) had not only the least intra-incremental variation in wood density, but also the least variation among trees.

In two southeastern Wyoming stands, Fahey (1983) found that standing dead lodgepole pine had stemwood specific gravities of 0.53 and 0.48 (probably based on oven-dry weight and air-dry volume, although not stated).

Hakkila and Panhelainen (1970) studied lodgepole pine 29 to 43 years old grown in Finland from seed originally obtained in Alberta and British Columbia. They found that an unbiased estimate of average stemwood density can be obtained from a knot-free sample taken at 20 percent of tree height, with the following equation ($R^2 = 0.828$; standard error of estimate 11.9 kg/m³):

$$Y = 117.6 + 0.723X$$

where:

Y = stemwood density based on oven-dry volume and weight, kg/m³

X = stemwood density at 20 percent of tree height.

Average stemwood specific gravity was 0.433. Standard deviation between stands in southern Finland was 3.1 percent of the mean. Specific gravity of stemwood in northern Finland at about 66.5 degrees latitude was 11.6 percent less than that in southern Finland at 60 to 62 degrees.

In a major study of specific gravity of lodgepole pine 5 inches and larger d.b.h. in the United States, Maeglin and Wahlgren (1972) took 3,516 breast-height increment cores throughout the Western States (*murrayana* as well as *latifolia*, but without distinguishing between varieties). From these cores they estimated tree stemwood specific gravities based on correlations determined from 213 trees, as follows ($R^2 = 0.749$; standard error of the estimate = 0.025):

$$\text{Tree stemwood specific gravity} = 0.06464 + 0.7617 (\text{core specific gravity})$$

The overall average for tree stemwood specific gravity on the basis of green volume and oven-dry weight was 0.379. Statistics for tree stemwood specific gravity and bulk density are given, by State, in table 4-1.

The Wood Handbook (USDA-FS 1974) gives 0.38 as the species average for lodgepole pine based on oven-dry weight and green volume.

Singh (1984) sampled 60 lodgepole pine trees, measuring 10 to more than 30 cm d.b.h., along a north-south gradient in Alberta. He found that average stemwood specific gravity was 0.444, with range from 0.376 to 0.539. Stemwood specific gravity was maximum at stump height (0.48), decreased to 0.44 at breast height and 0.43 in the upper merchantable stem, and then increased to 0.47 in the nonmerchantable stem top. Large branchwood of these trees had average specific gravity of 0.53. All data were based on oven-dry weights and oven-dry volumes.

Tackle (1962) concluded from a study of 44 dominant lodgepole pines in Idaho, Utah, and Wyoming, that tree-average stemwood specific gravity was 0.392 and ranged from 0.317 to 0.487 based on oven-dry weight and green volume. Stemwood specific gravity decreased significantly from stump height up to about 20 feet, but changed little above that. Tackle found that the relation of tree stemwood specific gravity to increment core specific gravity at

breast height was as follows ($r = 0.754$; standard error of estimate = 0.021):

$$\text{Stemwood specific gravity} = 0.143 + 0.661 (\text{core specific gravity})$$

Taylor and others (1982) studied two stands, one at high and one at low elevation, in each of three western Alberta Provincial Forests—one in the north, one in the south, and one midway between. Within each stand he sampled at breast height 10 dominant or codominant trees. Additionally, he sampled a total of six trees for variations within stems. All trees were 77 to 110 years old and 28 to 30 cm d.b.h. His determinations were made on an extractive-free basis, oven-dry weight and green volume. Trees from the three forests did not differ significantly in stemwood specific gravity at breast height; but differences between stands were significant, with range of means from 0.33 to 0.42 for rings 1 to bark. Within-stand variation between trees was also large. No differences between elevational zones were reported. Stemwood specific gravity decreased linearly with height above ground. Radial variation was different at different heights in the trees.

Diseases also affect stemwood specific gravity. In three even-aged stands—65, 67, and 95 years—of lodgepole pine in Alberta, Baranyay and others (1973) found that stemwood unaffected by *Atropellis* canker averaged 0.443 specific gravity based on oven-dry weight and green volume; wood portions infected by the canker disease had specific gravity of 0.715. Pitch and extractives content of the infected wood (38 percent of oven-dry weight) was largely responsible for the increased specific gravity noted. Also, stemwood of lodgepole pine parasitized by dwarf mistletoe has been found by Smythe (1967) to have significantly higher specific gravity than that of uninfected healthy wood.

Within-Stem Variation in Wood Specific Gravity—

Bjorklund (1982) found that lodgepole pine trees growing in Finland had stemwood specific gravity averaging 0.432 based on oven-dry weight and green volume. Stemwood specific gravity diminished with height in stems to 60 to 80 percent of tree height and then rose slightly in the uppermost stem section. Radially from the pith, density diminished initially and then increased. Intrastand variation was considerable and was inversely correlated with growth-ring width; that is, trees with wide rings had lower specific gravity than those with narrow rings.

The variation of stemwood specific gravity with height in 36 lodgepole pine trees averaging 4.3 inches in d.b.h. sampled near Prince George, BC, was studied by Heger (1974). He found a curvilinear variation with highest specific gravity at 10 percent height (0.428) and lowest at 70 percent height (0.395); at 90 percent height specific gravity increased slightly from the minimum to about 0.400.

Johnstone (1970a, 1970b) found from a study of 85-year-old lodgepole pine growing near Hinton, AB, that specific gravity decreased linearly from the base to the top of the trees if plotted against feet above ground (H), as follows ($R^2 = 0.137$; standard error of the estimate = 0.039):

$$\text{specific gravity} = 0.497 - 0.000854H$$

The relationship between tree stemwood specific gravity and that at breast height was as follows ($R^2 = 0.576$; standard error of estimate = 0.022):

$$\text{tree stemwood specific gravity} = 0.166 + 0.642 (\text{breast height specific gravity})$$

Mean stemwood specific gravity was 0.476, with standard deviation of 0.042 and range from 0.345 to 0.637.

From an analysis of three height classes of lodgepole pine broadly distributed in the Western United States (35-foot class, 10.6 inches d.b.h.; 50-foot class, 12.0 inches d.b.h.; and 65-foot class, 15.7 inches d.b.h.), Okkonen and others (1972) concluded that stemwood specific gravity declined more or less linearly with height above ground. In the two taller classes, the decline was less rapid above 20 feet than below 20 feet.

Additional findings related to within-tree variations in stemwood specific gravity are abstracted from Singh (1984), Tackle (1962), and Taylor and others (1982) under the preceding paragraph heading.

Sapwood and Heartwood—No data comparing heartwood to sapwood specific gravity were found in the literature.

Early Wood and Late Wood—From a study of 28-year-old lodgepole pine in Ireland, the Forest Products Laboratory, Princes Risborough (1960) found that there was no significant change in the specific gravity of late wood with height in stem, but early wood density decreased with increasing height in tree. Stem-average values for the two stands studied were:

Stemwood component	Stand A	Stand B
Late wood	0.51	0.54
Early wood	.30	.31
Entire ring	.36	.37

From 16 sites in New Zealand, Harris (1973) took increment cores at breast height from lodgepole pine trees 203 to 376 mm d.b.h. He found that the specific gravity of late wood increased more or less abruptly from the pith outward, but soon tended to settle at some nearly constant value between 0.5 and 0.7 depending on site. Early wood densities usually decreased over the first two to four growth increments and thereafter remained more or less constant between 0.30 and 0.35 depending on site. Weighted mean densities of the cores ranged from 0.362 to 0.453 depending on site (basis of oven-dry weight and green volume).

Henderson and Petty (1972) found significant differences in stemwood specific gravity between American coastal provenance material and Canadian inland provenance (Prince George) material grown in Scotland, as follows (data are from increment cores taken at 10 percent of tree height and are based on oven-dry weight and green volume):

Provenance	Early wood	Late wood	Entire increments
Prince George	0.30	0.56	0.39
Coastal U.S.	.33	.65	.47

Sylvander and Smith (1973), from an analysis of lodgepole pine throughout most of the interior of British Columbia—including that area adjacent to the Yukon

Territory—concluded that the specific gravity of stem early wood ranges from 0.36 to 0.43 while that of late wood is in the range from 0.57 to 0.70 based on oven-dry weight and green volume. They found a generally negative correlation between early wood increment width and early wood specific gravity, but did not find this trend uniformly in late wood. Specific gravity of entire annual rings tended to be negatively correlated with ring width.

Branches—In a western Wyoming study of lodgepole residues remaining after clearcut harvesting to a 6-inch merchantable top, Foulger and Harris (1973) found that bark of the residues had a specific gravity of 0.350 (basis of green weight and oven-dry volume) and that this value did not vary with diameter of the residues. Wood density, however, decreased from about 0.48 for material less than 0.6-inch diameter to about 0.38 for that larger than 3 inches.

As noted previously, Singh (1984) found that large branchwood from Alberta lodgepole had average specific gravity of 0.53, oven-dry weight and volume basis.

Bark—Smith and Kozak (1971) concluded from a study of lodgepole pine in British Columbia that the specific gravity of inner and outer stem bark was little influenced by tree d.b.h. Specific gravity of inner bark averaged 0.335 and that of outer bark 0.508—both based on oven-dry weight and green volume. These values were derived from specimens taken at 30- and 137-mm heights in 22 trees measuring 280 mm in d.b.h.

See comments under the preceding paragraph heading regarding the specific gravity of branch bark.

Stump-Root System—No data were found in the literature related to specific gravity of lodgepole pine stump-root systems.

Weight of Tree Components per Hectare

Not within the scope of this paper, but of peripheral interest, are weights per hectare of lodgepole pine biomass. Following is a listing of pertinent references with an indication of content.

Benson (1982) evaluated ground fuels in Wyoming, by component weight, before and after logging. Brown and others (1977) described procedures to predict slash weights per hectare on the basis of basal area or number of trees per hectare. Fahnestock and Dieterich (1962) tabulated the reduction in fuel weight on the forest floor 1 and 5 years after harvest. Kiil (1968) studied the weight per hectare of the fuel complex in a 70-year-old stand in Alberta.

Moir (1972) tabulated—per unit area—stand biomass of bole, live branches, roots, green needles, cones, dead branches, standing dead timber, forest floor humus, and ground flora on the east slopes of the Colorado Front Range.

Muraro (1971) tabulated the number of live and dead trees per acre and tons per acre of fuel on the ground based on 160 sampling points in a variety of lodgepole pine associations 20 miles south of Merritt, BC. In an earlier publication describing the same area Muraro (1966) tabulated per-acre tonnage of slash, foliage, branchwood, and tops.

Pearson (1982) found in a study of stands 70 years old or older in southeastern Wyoming that biomass ranged

from 116 to 175 tons per hectare, ovendry basis; of this total, woody roots accounted for 20 to 46 t/ha.

Peterson and others (1982) studied the upper limits of density, expressed as kilograms per cubic meter of a standing crop of lodgepole pine. Reynolds and Knight (1973) found that litter in lodgepole pine forests in Wyoming weighed 12,113 kg/ha, ovendry basis.

Roydhouse and others (1985), from data on 20-year-old fire-originated stands near Williams Lake, BC, related biomass per hectare to number of stems per hectare, as follows:

Stems/ha	Aboveground biomass, ovendry kg/ha
150,000	27,500
50,000	53,000
20,000	52,000
5,000	45,000

These references, and conversations with experienced technologists, suggest that a typical well-stocked stand of lodgepole pine 80 to 150 years old on a typical site has stemwood volume (stump top to apical tip) in standing live trees of about 104 t/ha, and perhaps 26 t/ha of standing dead stemwood for a total of 130 t/ha of stemwood—ovendry basis. Total aboveground biomass—live and standing dead, including foliage—typically totals about 166 t/ha, ovendry basis.

4-4 PROCEDURE

Procedural details of the experiment are given in chapter 1, and will not be repeated here except to note that the elevational zones of low, medium, and high are relative. Medium refers to an elevation that is medium for the variety at the latitude at which sampled; similarly, low and high refer to lower and upper elevational zones in which the variety occurs at the latitude sampled. *Latifolia* elevational zones were highest in the south (2,481, 2,711, and 3,144 m at 40 degrees) and progressively lower with each more northerly latitude (604, 739, and 879 m at 60 degrees). *Murrayana* was sampled at elevations in the range from 1,148 to 2,404 m.

Trees were uprooted (with central taproot intact and with lateral roots severed at a radius of 305 mm from tree pith) from level benches in natural, unthinned stands within National or Provincial Forests. The sampling scheme resulted in selection of 76-, 152-, and 228-mm trees averaging 71, 91, and 107 years of age, respectively, for *latifolia*, and 67, 84, and 91 years for *murrayana*. Most of the small-diameter trees were suppressed, while the larger trees were the fast growers. Stump tops were 152 mm above ground level.

4-5 RESULTS—LATIFOLIA

In the following paragraphs summarizing results, only those main effects and interactions shown statistically significant (0.05 level) by analyses of variance are discussed, tabulated, and graphed. All reported correlations are statistically significant (0.05 level).

Average specific gravities of tree components are summarized in table 4-2, weights in table 4-3, major tree com-

Table 4-2—Average specific gravities (basis of ovendry weight and green volume), with standard deviations shown in parentheses, of lodgepole pine tree components; data are from 243 *latifolia* and 36 *murrayana* trees¹

Tree component	Variety	
	<i>Latifolia</i>	<i>Murrayana</i>
Complete tree without cones and foliage		
Wood plus bark	0.421 (0.028)	0.438 (0.037)
Wood	.428 (.030)	.449 (.043)
Bark	.381 (.040)	.379 (.033)
Live branches		
Wood plus bark	.457 (.031)	.458 (.024)
Branchwood	.487 (.036)	.494 (.022)
Branchbark	.411 (.051)	.414 (.048)
Stem		
Wood plus bark	.412 (.030)	.433 (.041)
Stemwood	.418 (.032)	.433 (.048)
Stembark	.369 (.042)	.361 (.029)
Sapwood	.414 (.034)	.437 (.048)
Heartwood	.434 (.034)	.502 (.067)
Stump-root system		
Wood plus bark	.461 (.043)	.461 (.045)
Wood	.469 (.045)	.467 (.050)
Bark	.415 (.056)	.412 (.043)
Stump		
Wood plus bark	.471 (.046)	.496 (.054)
Wood	.476 (.051)	.506 (.063)
Bark	.445 (.064)	.431 (.055)
Lateral roots		
Wood plus bark	.442 (.047)	.432 (.066)
Wood	.453 (.048)	.443 (.072)
Bark	.399 (.082)	.388 (.059)
Central root mass-taproot		
Wood plus bark	.468 (.052)	.457 (.051)
Wood	.475 (.055)	.460 (.055)
Bark	.425 (.066)	.426 (.057)

¹Because of the effects and interactions of d.b.h., latitude, and elevational zone, reference to appropriate figures and text discussion is required for interpretation of these data.

ponent proportions of weight in table 4-4, bark weight proportions of tree components in table 4-5, and green weights of the three major tree components required to yield 1 m³ of wood in table 4-6. Interpretation of these averages requires reference to the main effects and interaction attributable to d.b.h., latitude, and elevational zone—as discussed in the following paragraphs.

Longitudinal effects on *latifolia* were confounded with latitudinal effects (the northern latitudinal zones were farther west than the southern latitudinal zones). When each latitudinal zone was divided into 10 longitudinal zones, each a degree of longitude wide and expressed by a number from 1 to 10 going from east to west, only two significant relationships were observed in which the correlation coefficients exceeded 0.20. Average weights, green and ovendry, of cones taken from the tip 305 mm of the top 25 branches of each tree were negatively correlated with longitudinal zone ($r = -0.394$ and -0.428 , respectively); that is, individual cone weights from trees on the east end of the latitudinal zones averaged more than those on the west end.

Table 4-3—Average weights—green and ovendry—of lodgepole pine tree components, with data from the 243 *latifolia* and the 36 *murrayana* trees by d.b.h. classes of 76, 152, and 228 mm¹

Tree component	Green			Ovendry		
	76	152	228	76	152	228
----- Kilograms -----						
<i>Latifolia</i>						
Complete tree with foliage	28.40	170.46	440.19	14.51	87.30	227.73
Tree wood	21.88	141.11	370.58	11.42	72.55	191.17
Tree bark	3.91	17.34	39.17	1.84	8.69	20.57
Foliage	2.47	11.05	26.71	1.14	5.28	12.90
Cones, tree total ²	.14	.96	3.74	.11	.78	3.09
Cones, individual ³	0.0052	0.0060	0.0068	0.0042	0.0048	0.0056
Dead branchwood	.32	2.03	5.76	.26	1.65	4.87
Live branches						
Wood plus bark	1.31	9.07	31.92	.67	4.62	16.32
Wood	.74	5.93	23.14	.39	3.11	12.09
Bark	.57	3.14	8.80	.28	1.51	4.23
Stem						
Wood plus bark	20.34	128.49	328.84	10.35	65.15	168.12
Stemwood	17.63	116.62	303.01	9.14	59.13	154.08
Stembark	2.71	11.87	25.83	1.27	6.02	14.04
Sapwood	14.37	91.34	226.16	6.89	41.45	99.81
Heartwood	3.26	25.28	76.85	2.25	17.86	54.27
Stump-root system						
Wood plus bark	3.82	18.86	43.22	1.91	9.82	22.43
Wood	3.19	16.53	38.67	1.61	8.66	20.13
Bark	.63	2.33	4.54	.30	1.16	2.30
Stump						
Wood plus bark	1.15	3.67	7.18	.59	2.01	3.89
Wood	.98	3.28	6.51	.50	1.76	3.45
Bark	.17	.43	.72	.09	.25	.44
Lateral roots						
Wood plus bark	1.05	6.75	15.53	.51	3.37	7.80
Wood	.81	5.72	13.45	.40	2.88	6.82
Bark	.24	1.03	2.08	.11	.49	.98
Central root mass-taproot						
Wood plus bark	1.62	8.40	20.47	.81	4.45	10.74
Wood	1.40	7.54	18.72	.71	4.02	9.86
Bark	.22	.86	1.75	.10	.43	.88

(con.)

Table 4-3 (Con.)

Tree component	Green			Ovendry		
	76	152	228	76	152	228
----- Kilograms -----						
<i>Murrayana</i>						
Complete tree with foliage	24.25	151.57	419.37	12.11	72.95	197.65
Tree wood	19.01	127.59	362.34	9.74	61.44	161.91
Tree bark	3.39	15.54	36.37	1.51	7.36	17.77
Foliage	1.81	8.19	19.83	.83	3.94	9.28
Cones, tree total ²	.04	.25	.83	.03	.21	.69
Cones, individual ³	0.0037	0.0052	0.0049	0.0031	0.0044	0.0041
Dead branchwood	.26	1.08	4.91	.21	.89	4.34
Live branches						
Wood plus bark	1.25	7.85	28.15	.65	4.34	13.82
Wood	.63	4.82	18.58	.35	2.69	9.37
Bark	.62	3.03	9.57	.30	1.65	4.45
Stem						
Wood plus bark	17.16	113.41	321.69	8.59	54.17	149.05
Stemwood	14.98	103.41	298.80	7.63	49.46	137.55
Stembark	2.18	10.00	22.89	.96	4.71	11.50
Sapwood	13.60	88.54	253.53	6.74	39.00	105.30
Heartwood	1.38	14.87	45.27	.95	10.46	32.25
Stump-root system						
Wood plus bark	3.75	20.53	43.87	1.80	9.70	20.56
Wood	3.16	18.14	39.96	1.55	8.59	18.73
Bark	.59	2.39	3.91	.25	1.11	1.83
Stump						
Wood plus bark	1.25	4.57	6.80	.65	2.30	3.28
Wood	1.09	4.15	6.27	.58	2.08	2.98
Bark	.16	.42	.53	.07	.22	.30
Lateral roots						
Wood plus bark	.63	6.25	15.65	.28	2.80	7.11
Wood	.47	5.25	13.79	.22	2.38	6.31
Bark	.16	1.00	1.86	.06	.42	.80
Central root mass-taproot						
Wood plus bark	1.87	9.72	21.42	.87	4.60	10.18
Wood	1.60	8.74	19.90	.76	4.13	9.45
Bark	.27	.98	1.52	.11	.47	.73

¹Because of the effects of latitudinal and elevational zones, reference to appropriate figures and text discussion is required for interpretation of these data. Components may not total exactly because of computational and rounding procedures.

²Calculated.

³From tip 305 mm of top 25 branches.

Table 4-4—Tree component proportions of complete-tree weight, green and ovendry, with data from the 243 *latifolia* and 36 *murrayana* trees by d.b.h. classes of 76, 152, and 228 mm¹

Tree component and moisture content	<i>Latifolia</i>			<i>Murrayana</i>		
	76	152	228	76	152	228
----- Percent -----						
Foliage (including branches to 6-mm diameter)						
Green	8.7	6.6	6.1	7.6	5.8	5.0
Ovendry	8.2	6.3	5.8	7.1	6.0	5.0
Cones						
Green	.5	.6	.9	.1	.2	.2
Ovendry	.7	.9	1.4	.2	.3	.4
Live branches (wood plus bark)						
Green	4.6	5.4	7.4	5.2	5.6	7.3
Ovendry	4.8	5.5	7.3	5.6	6.8	7.8
Dead branches						
Green	1.2	1.2	1.3	1.1	.8	1.2
Ovendry	1.9	1.9	2.2	1.8	1.3	2.2
Stem (wood plus bark) from 152-mm stump height to apical tip						
Green	71.5	75.1	74.4	70.4	73.4	75.6
Ovendry	71.0	74.0	73.4	70.3	72.3	73.9
Stump-root system (wood plus bark) with laterals to a radius of 305 mm from stump pith						
Green	13.5	11.2	9.9	15.6	14.0	10.7
Ovendry	13.3	11.4	10.0	15.0	13.8	10.7
Total ²						
Green	100.0	100.1	100.0	100.0	99.8	100.0
Ovendry	99.9	100.0	100.1	100.0	100.5	100.0

¹Because of the interactions of d.b.h., latitude, and elevational zone on these properties, reference to appropriate figures and text discussion is needed for interpretation of these data. For weight proportions of sapwood and heartwood see chapter 5.

²Totals may not sum to exactly 100.0 due to rounding errors.

Table 4-5—Bark weight proportions, green and ovendry, of major lodgepole pine tree components, with data from 243 *latifolia* and 36 *murrayana* trees by d.b.h. classes of 76, 152, and 228 mm

Tree component and moisture content	<i>Latifolia</i>			<i>Murrayana</i>		
	76	152	228	76	152	228
----- Percent -----						
Bark of foliage-free complete tree, percent of gross foliage-free complete-tree weight						
Green	15.3	11.1	9.7	15.3	11.3	9.4
Ovendry	14.1	10.9	9.8	13.7	11.3	10.0
Stembark percent of gross stem weight, stump top to apical tip						
Green	13.5	9.3	7.9	12.9	9.1	7.3
Ovendry	12.4	9.4	8.4	11.4	9.2	8.0
Live branchbark percent of gross live branch weight						
Green	44.1	35.0	28.0	49.5	38.4	32.2
Ovendry	41.8	33.2	26.4	47.4	37.8	30.7
Stump-root bark percent of gross stump-root weight						
Green	16.5	12.3	10.6	15.7	11.5	8.9
Ovendry	15.5	11.9	10.2	13.8	11.5	9.0

Table 4-6—Green weights of the three major tree components required to yield 1 m³ of wood for *latifolia* and *murrayana* of three diameters¹

Tree component (wood plus bark), and d.b.h., mm	Weight	
	<i>Latifolia</i>	<i>Murrayana</i>
----- Kilograms -----		
Foliage-free branches		
76	1,649	1,854
152	1,427	1,584
228	1,267	1,416
Stems		
76	968	1,093
152	920	1,030
228	872	968
Stump-root systems²		
76	1,109	1,156
152	1,044	1,110
228	984	1,061

¹Because of the interactions of d.b.h., latitude, and elevational zone on these yields, reference to appropriate figures and text discussion is needed for interpretation of these data. Data are based on 243 *latifolia* and 36 *murrayana* trees.

²Based on stumps to a 152-mm height, lateral roots to a radius of 305 mm from stump pith, and as much of the taproots as the field crews were able to extract; see figure 1-4.

With data from each longitudinal zone averaged, mean ovendry weights per cone varied as follows (zone 1 is the easternmost zone and zone 12 is westernmost):

Longitudinal zone	Average weight per cone, ovendry	Number of trees with cones per zone
	Grams	
1	6.90	10
2	9.13	4
3	6.31	21
4	4.55	22
5	5.89	12
6	4.64	26
7	5.60	27
8	4.04	13
9	4.17	25
10	4.40	15
11	3.45	13
12	2.97	3

The 16 cone-bearing trees in longitudinal zones 11 and 12 were slightly to the west of intended sampling areas because of scarce roads in northern Canada. As previously noted, each longitudinal zone was 1 degree wide; northern zones therefore spanned less distance than southern zones.

The foregoing data, if used to predict weight of individual cones on the tip 305 mm of the top 25 branches, yields the following equation ($R^2 = 0.713$; standard error of estimate = 0.96 g):

Ovendry weight/cone =
 $7.76508 - 0.39918 (\text{longitudinal zone number})$

Correlations Between Moisture Content and Specific Gravity of Tree Components

As described in chapter 2, throughout the full range of latitude (40 to 60 degrees) in which moisture contents were studied, there was a pronounced decrease in *latifolia* tree-component moisture content from south to north. Maximum moisture contents usually occurred at latitude 42.5 or 45 degrees, and minimums were observed between 52.5 and 60 degrees. For example, stemwood moisture content (diameter data pooled) averaged 124 percent at 42.5 degrees and only 83 percent at 60 degrees. Similarly, stembark moisture content averaged 131 percent at 45 degrees, but only 80 percent at 52.5 degrees.

This variation in tree component moisture content is explained to a significant degree by the inverse relationship between moisture content and specific gravity; that is, wood or bark of high specific gravity tends to have low moisture content. The correlation coefficients were found to be between -0.6 and -0.9, with generally higher correlations for bark than for wood (table 4-7).

With data from all wood components of *latifolia* pooled, the following regression equation applies ($R^2 = 0.367$; standard error of the estimate = 18.421):

Wood moisture content, percent of ovendry weight =
 $295.90 - 467.52 (\text{wood specific gravity, ovendry weight and green volume})$

For all bark components pooled, the following equation applies ($R^2 = 0.693$; standard error of the estimate = 14.055):

Bark moisture content, percent =
 $305.43 - 530.80 (\text{bark specific gravity})$

Table 4-7—Correlations between moisture content and specific gravity of components of 243 *latifolia* trees (all diameter, latitudinal, and elevational data pooled)

Tree component	Wood plus bark	Wood	Bark
----- Correlation coefficient, r -----			
Complete tree (without foliage and cones)	-0.665	-0.606	-0.832
Stem from 152-mm stump height to apical tip	-.641	-.600	-.820
Live branches	-.753	-.629	-.858
Stump-root system, entire, to a radius of 305 mm from stump pith	-.632	-.613	-.701
Stump, groundline to 152-mm height	-.674	-.659	-.699
Lateral roots, root collar to 152-mm radius from stump pith	-.776	-.725	-.579
Central root mass including taproot	-.779	-.738	-.685

Stemwood Specific Gravity Correlations

In addition to the correlation with stemwood moisture content, the following significant correlations of entire stemwood specific gravity (basis of oven-dry weight and green volume) with other tree statistics are of interest:

Statistic	r
Moisture content of complete tree with foliage	-.0569
Live-branch weight (wood plus bark) as percentage of gross complete-tree weight including foliage—oven-dry basis	-.416
Stem (wood plus bark) as percentage of gross complete-tree weight including foliage—oven-dry basis	.400
Sapwood thickness at 152-mm stump height	-.384
Foliage as percentage of complete-tree weight—oven-dry basis	-.381
Crown ratio	-.358
Elevation, m	-.357
Stem diameter at base of live crown, inside bark	-.355
Average stem taper below live crown, inside bark, mm/m	-.346
Stembark specific gravity	.318
Average growth-ring width at 152-mm stump height	-.313
Average live branch angle	.306
Foliage weight, oven-dry	-.302
Heartwood volume as percentage of stem-wood volume	.282
Average diameter of live branches	-.282
Length of live crown	-.272
Live-branch weight, wood plus bark—oven-dry basis	-.255
D.b.h.	-.254
Diameter at 152-mm stump height	-.238
Width of live crown	-.225
Dead-branch weight—oven-dry	-.167

In the foregoing tabulation, 17 of the 21 are negative correlations. These negative correlations suggest that low stemwood specific gravity will be found at high elevation in vigorously growing large trees with thick sapwood, high moisture content, long and wide crowns with large branches and heavy foliage, highly tapered stems below crown, and wide growth rings.

Conversely, higher stemwood gravities will be found at lower elevations in smaller, slower growing trees with large branch angles, stembark of high specific gravity, and stems that constitute a high proportion of complete-tree weight, and in which heartwood percentage of stemwood volume is high.

Because growth-ring width is an easily measured parameter, it is useful to have a predictive equation relating stemwood specific gravity to average growth-ring width, as follows ($R^2 = 0.074$; standard error of the estimate = 0.038):

$$G = 0.4780 - 0.0228W$$

where:

- G = stemwood specific gravity at 152-mm stump height, basis of oven-dry weight and green volume
 W = average growth-ring width at 152-mm stump height, mm.

Readers are cautioned that this relationship is weak, and that it pertains only to stemwood at 152-mm stump height—where, with all data pooled, stemwood specific gravity averaged 0.455 and average growth-ring width averaged 1.00 mm; it is not applicable to higher stem positions.

Stembark Specific Gravity Correlations

In addition to the correlation with stembark moisture content, the following significant correlations of entire stembark specific gravity (basis of oven-dry weight and green volume) with other tree characteristics are of interest:

Statistic	r
Moisture content of complete tree with foliage	-.0581
Heartwood volume as percentage of stem-wood volume	.554
Foliage weight as percentage of complete-tree weight—oven-dry basis	-.531
Crown ratio	-.497
Heartwood diameter at 152-mm stump height	.466
Stem (wood plus bark) as percentage of complete-tree weight including foliage—oven-dry basis	.408
Tree age at 152 mm stump height	.364
Tree height to apical tip	.358
Bark thickness at 152 mm stump height	.343
Stem weight, wood plus bark, oven-dry	.329
Stemwood specific gravity	.318
Stump-root system weight, wood plus bark, oven-dry	.313
Average taper within crown, inside bark, mm/m	.309
Complete-tree weight, including foliage, oven-dry	.308
Diameter outside bark at 152-mm stump height	.306
D.b.h.	.277
Average diameter of live branches	.228
Number of cones on the tip 305 mm of the top 25 branches	.218
Width of live crown	.198
Live-branch weight (wood plus bark) as percentage of complete-tree weight including foliage—oven-dry basis	-.192
Live-branch weight, wood plus bark, oven-dry	.173
Elevation, m	-.167

These data suggest that stembark of high specific gravity is likely to be found at lower elevations in taller,

older, and larger thick-barked trees of low moisture content, with short and narrow crowns, little foliage but many cones on the top 25 branches, large stump-root systems, large branches, stemwood of high specific gravity and a high percentage of heartwood volume, and with stems constituting a high percentage of complete-tree weight.

Correlations of the Six Major Tree Component Weight Percentages of Complete-Tree Owendry Weight (Including Foliage) With Other Tree Properties

Stem, Wood Plus Bark—The following significant correlations with stem weight as a percentage of complete-tree owendry weight are of interest:

Statistic	<i>r</i>
Foliage weight as percentage of complete-tree weight—owendry basis	–0.792
Live-branch weight (wood plus bark) as percentage of complete-tree weight including foliage—owendry basis	–.710
Crown ratio	–.609
Tree height to apical tip	.514
Heartwood volume as percentage of stemwood volume	.477
Moisture content of complete tree with foliage	–.472
Stump-root system weight (wood plus bark) as percentage of complete-tree weight including foliage—owendry basis	–.454
Stembark specific gravity	.408
Stemwood specific gravity	.400
Average stem taper, inside bark, to base of live crown, mm/m	–.386
Heartwood diameter at 152-mm stump height	.292
Dead-branch weight as percentage of complete-tree weight with foliage—owendry basis	–.292
Weight of stem, wood plus bark, owendry	.282
Tree age at 152-mm stump height	.249
Cone weight as percentage of complete-tree weight with foliage—owendry basis	–.220
Complete-tree weight including foliage, owendry	.195
Sapwood thickness at 152-mm stump height	–.190
Live-branch weight, wood plus bark, owendry	–.168

Thus, aside from the obvious correlation with weight percentages of the other tree components, stem weight percentage is highest in older and taller trees with high stemwood and stembark specific gravities, low crown ratios, low moisture content, little stem taper below the crown, a high percentage of heartwood volume in the stem, and thin sapwood.

Foliage—The following significant correlations with foliage weight as a percentage of complete-tree weight are of interest:

Statistic	<i>r</i>
Stem (wood plus bark) as percentage of complete-tree weight with foliage—owendry basis	–0.792
Crown ratio	.668
Heartwood volume as percentage of stemwood volume	–.626
Moisture content of complete tree with foliage	.614
Stembark specific gravity	–.531
Tree height to apical tip	–.508
Live-branch (wood plus bark) weight as percentage of complete-tree weight with foliage—owendry basis	.491
Heartwood diameter at 152-mm stump height	–.458
Stemwood specific gravity	–.381
Weight of stem, wood plus bark, owendry	–.357
Complete-tree weight with foliage, owendry	–.308
Weight of stump-root system, wood plus bark, owendry	–.285
Tree age at 152-mm stump height	–.272
D.b.h.	–.272
Stump-root system (wood plus bark) as percentage of complete-tree weight with foliage—owendry basis	.266
Diameter outside bark at 152-mm stump height	–.259
Average stem taper within crown, inside bark, mm/m	–.233
Elevation, m	.231
Average stem taper below crown, inside bark, mm/m	.229
Taproot length (portion recovered)	–.194
Number of cones on tip 305 mm of top 25 branches	–.181
Dead-branch weight, owendry	–.173
Average diameter of live branches	–.167

These data suggest that foliage comprises the highest percentage of complete-tree owendry weight in young, small trees growing at higher elevations with high crown ratios, high complete-tree moisture content, low heartwood volume percentage of stemwood volume, low stemwood and stembark specific gravities, little stem taper within crown but high taper below crown, small average branch diameter, few cones on the top 25 branches, and a low percentage of stem weight but a high percentage of live-branch weight. Trees with a high proportion of their weight in the central stump-root system also tend to have a high proportion of foliage weight.

Cones—The following significant correlations with cone weight percentage of complete-tree owendry weight are of interest. The cone weights per tree were calculated from data on cones found on the tip 305 mm of the top 25 branches, as described in the procedure section of chapter 1.

Statistic	r
Stem (wood plus bark) as percentage of complete-tree weight with foliage—ovendry basis	−0.220
Foliage weight, ovendry	.207
Average diameter of live branches	.206
Average stem taper within crown, inside bark, mm/m	.205
Diameter outside bark at 152-mm stump height	.202
D.b.h.	.191
Stem diameter at base of live crown, inside bark	.187
Complete-tree weight with foliage, ovendry	.186
Heartwood diameter at 152-mm stump height	.183
Stump-root system weight, wood plus bark, ovendry	.182
Live-branch weight, wood plus bark, ovendry	.168

These correlations should be interpreted with caution, because they were based on a computed ovendry weight of cones per tree, rather than on direct measurement.

The data suggest, however, that cones attain highest proportion of complete-tree ovendry weight on large-diameter trees with heavy stump-root systems, highly tapered stems within crowns, heavy foliage, large-diameter branches, large heartwood diameter at stump height, and a low proportion of complete-tree weight in the stem.

Live Branches, Wood Plus Bark—The following significant correlations with foliage-free live-branch weight percentage of complete-tree ovendry weight are of interest:

Statistic	r
Stem (wood plus bark) as percentage of complete-tree weight with foliage—ovendry basis	−0.710
Live-branch weight, wood plus bark, ovendry	.660
Width of live crown	.585
Foliage weight, ovendry	.552
Average stem taper, inside bark, to base of live crown, mm/m	.550
Stem diameter at base of live crown, inside bark	.507
Crown ratio	.492
Foliage weight as percentage of complete-tree weight—ovendry basis	.491
Sapwood thickness at 152-mm stump height	.460
Average diameter of live branches	.423
Stemwood specific gravity	−.416
Average growth-ring width at 152-mm stump height	.393
D.b.h.	.345
Diameter outside bark at 152-mm stump height	.343

(con.)

Statistic	r
Moisture content of complete tree with foliage	.341
Length of live crown	.326
Dead-branch weight, ovendry	.312
Weight of stump-root system, wood plus bark, ovendry	.311
Complete-tree weight, ovendry	.272
Bark thickness at 152-mm stump height	.268
Heartwood volume as percentage of stem-wood volume	−.231
Number of live branches	.226
Average live-branch angle	−.223
Taproot length (portion recovered)	.201
Dead-branch weight as percentage of complete-tree weight with foliage, ovendry basis	.199
Stembark specific gravity	−.192
Weight of stem, wood plus bark, ovendry	.182

Aside from the obvious increase in live-branch weight as a percentage of complete-tree weight caused by numerous large, heavy branches in big crowns, other correlations suggest that live branches comprise the highest weight proportion of complete trees in large-diameter, heavy, fast-growing trees with high moisture content, heavy foliage, heavy dead branches, large stem diameter at the base of the live crown, highly tapered stems, thick sapwood, thick bark, and heavy stump-root systems with long taproots. Live-branch weight proportion was negatively correlated with stemwood and stembark specific gravities, heartwood volume as percentage of stemwood volume, average branch angle, and with proportion of complete-tree weight in the stem.

Dead Branches—The following significant correlations with dead-branch weight as percentage of complete-tree weight are weak, but of interest:

Statistic	r
Dead-branch weight, ovendry	0.697
Stem (wood plus bark) weight as percentage of complete-tree weight, ovendry basis	−.292
Average growth-ring width at 152-mm stump height	.230
Live-branch (wood plus bark) weight as percentage of complete-tree weight, ovendry basis	.199
Average stem taper to base of live crown, inside bark, mm/m	.195
Elevation, m	−.182
Average live branch angle	−.168

These data suggest that dead-branch weight as a percentage of complete-tree weight is highest in low-elevation, fast-growing trees with a high percentage of live-branch weight, small average live-branch angle, highly tapered stems below crown, and a low proportion of complete-tree weight in the stem.

Stump-Root System, Wood Plus Bark—The following significant correlations with stump-root system weight percent of complete-tree ovendry weight are of interest:

Statistic	<i>r</i>
Tree height from 152-mm stump height to apical tip	−0.629
Complete-tree weight, including foliage, ovendry	−.522
Weight of stem, wood plus bark, ovendry D.b.h.	−.537
	−.506
Diameter outside bark at 152-mm stump height	−.480
Number of live branches	−.455
Stem (wood plus bark) as percentage of complete-tree weight with foliage—ovendry basis	−.454
Heartwood diameter at 152-mm stump height	−.441
Stem diameter at base of live crown, inside bark	−.418
Foliage weight	−.403
Stump-root weight, wood plus bark, ovendry	−.381
Live-branch weight, wood plus bark, ovendry	−.377
Width of live crown	−.362
Length of live crown	−.344
Average diameter of live branches	−.338
Sapwood thickness at 152-mm stump height	−.321
Dead-branch weight, ovendry	−.287
Foliage as percentage of complete-tree weight—ovendry basis	.266
Number of cones on the tip 305 mm of the top 25 branches	−.265
Bark thickness at stump height	−.261
Average growth-ring width at 152-mm stump height	−.244
Tree age at 152-mm stump height	−.221
Taproot length (portion recovered)	−.217
Average live-branch angle	−.199

All of these correlation coefficients are negative, with the exception of that for foliage as a percentage of complete-tree weight; even taproot length and weight of

the stump-root system are negatively correlated with the weight percentage of the stump-root system.

If a high percentage of complete-tree weight in the stump-root system was desired (perhaps for naval stores manufacture from paraquat-enriched oleoresin content), such percentage would likely be highest in young, slow-grown, small trees with small crowns, few branches, little foliage, little dead-branch weight, and thin stem bark.

Complete Tree With Cones and Foliage

Weight, Green—Green weight of complete trees with stump-root system and foliage was positively correlated with d.b.h., averaging 28.40 (4.99), 170.46 (27.61), and 440.19 (65.31) kg for trees 76, 152, and 228 mm in d.b.h. In general, trees in high-elevation zones weighed less than those in low-elevation zones; for example, complete trees 228 mm in d.b.h. weighed 468.32, 439.63, and 412.62 kg in low-, medium-, and high-elevation zones, respectively.

With diameter and elevation data pooled, complete trees averaged least weight (195.11 kg) in the southernmost latitudinal zone and were heaviest in latitudes 50 to 55 degrees—where they averaged 227.09 kg, but relationships varied with diameter and elevational zone (fig. 4-1).

Weight, Ovendry—Ovendry weight of complete trees with stump-root system and foliage was positively correlated with d.b.h., averaging 14.51 (2.90), 87.30 (15.96), and 227.72 (34.71) kg for the three diameter classes.

Complete-tree weight was negatively correlated with elevational zone (fig. 4-2), as summarized by the following tabulation of average tree weights by d.b.h.:

Elevational zone	Diameter class		
	76 mm	152 mm	228 mm
	----- Kilograms -----		
Low and medium	14.62	89.66	235.46
High	14.29	82.57	212.26

With diameter and elevational data pooled, average tree weight was lowest (99.49 kg) in the three southernmost latitudinal zones—40 through 45 degrees, and highest (119.41 kg) from 47.5 through 55 degrees; in the northernmost latitudes of 57.5 and 60 degrees, average tree weight was intermediate (106.25 kg). (See figure 4-2.)

LATIFOLIA

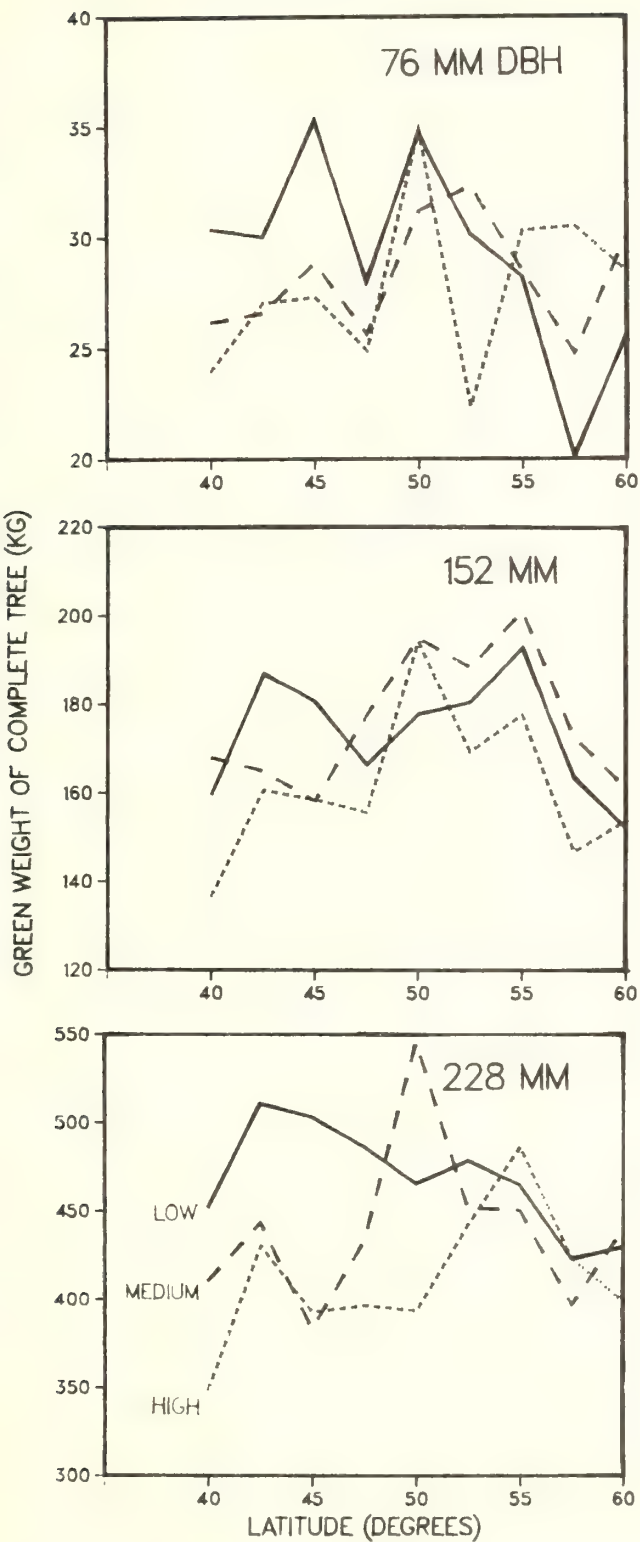


Figure 4-1—Green weight of complete *latifolia* trees of three diameters (including foliage and stump-root system) related to latitude and elevational zone.

LATIFOLIA

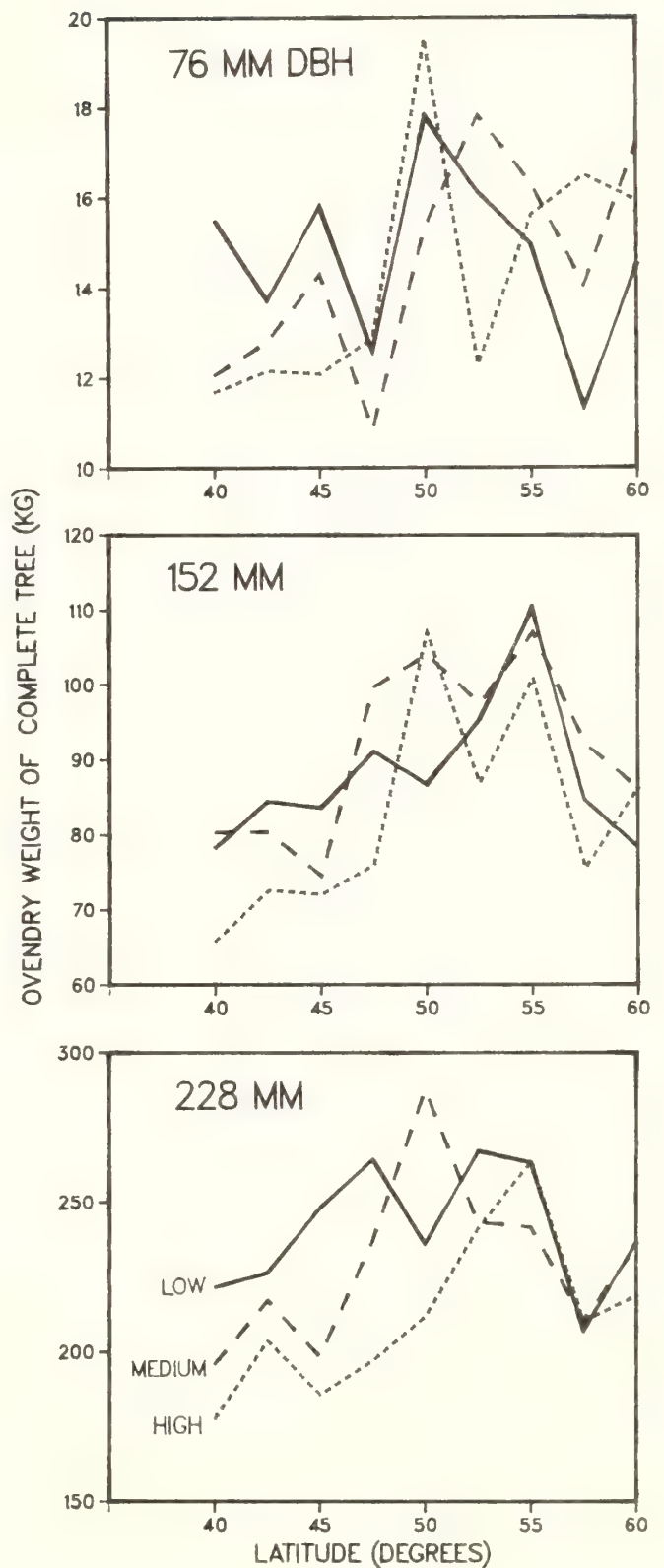


Figure 4-2—Ovendry weight of complete *latifolia* trees of three diameters (including foliage and stump-root system) related to latitude and elevational zone.

Complete Tree Without Cones or Foliage

Specific Gravity—Wood plus bark of the complete trees (foliage-free branches, stem, and stump-root system) had average specific gravity, based on ovendry weight and green volume, of 0.421 with standard deviation of 0.028. It was unrelated to elevational zone, but was—in northern latitudes—negatively correlated with d.b.h.; overall averages were 0.425 (0.034), 0.423 (0.026), and 0.416 (0.024) for trees 76, 152, and 228 mm in d.b.h.—a relationship unusual in conifers.

Variation with latitude (fig. 4-3) was inverse to that of moisture content (fig. 2-3). Average specific gravity was lowest (0.397) at 42.5 degrees latitude, and increased with increasing latitude to maximums (0.430 or more) in latitudes 47.5 through 55 degrees and at 60 degrees (fig. 4-3).

Weight, Green—Without foliage, green weights of complete trees 76, 152, and 228 mm in d.b.h. averaged 25.93 (4.71), 159.41 (27.31), and 413.48 (64.42) kg. Green-weight variation with latitude was not pronounced (fig. 4-4); evidently the lower moisture content of trees in northern latitudes (fig. 2-3) offsets the greater ovendry weight of the northern trees (fig. 4-5). Green weight was negatively correlated with elevational zone, however, averaging 209.88, 201.76, and 187.17 kg in low, medium, and high zones, respectively (diameter data pooled).

Weight, Ovendry—Without foliage, weights of ovendry trees of the three diameter classes averaged 13.37 (3.00), 82.02 (16.41), and 214.82 (35.44) kg. With diameter data pooled, trees in low- and medium-elevation zones averaged heavier (106.82 kg) than those in high zones (96.57 kg). In contrast with green-basis weights, weights of ovendry trees increased significantly from south to north (fig. 4-5); weights averaged maximum at 55 degrees (119.74 kg) and minimum at 40 degrees (88.85 kg).

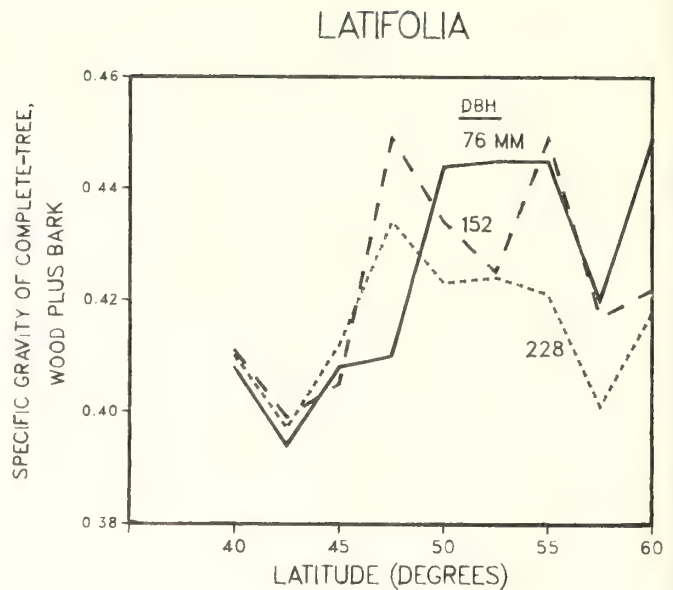


Figure 4-3—Specific gravity based on ovendry weight and green volume of foliage-free complete *latifolia* trees of three diameters, including wood plus bark of branches, stem, and stump-root system related to latitude.

LATIFOLIA

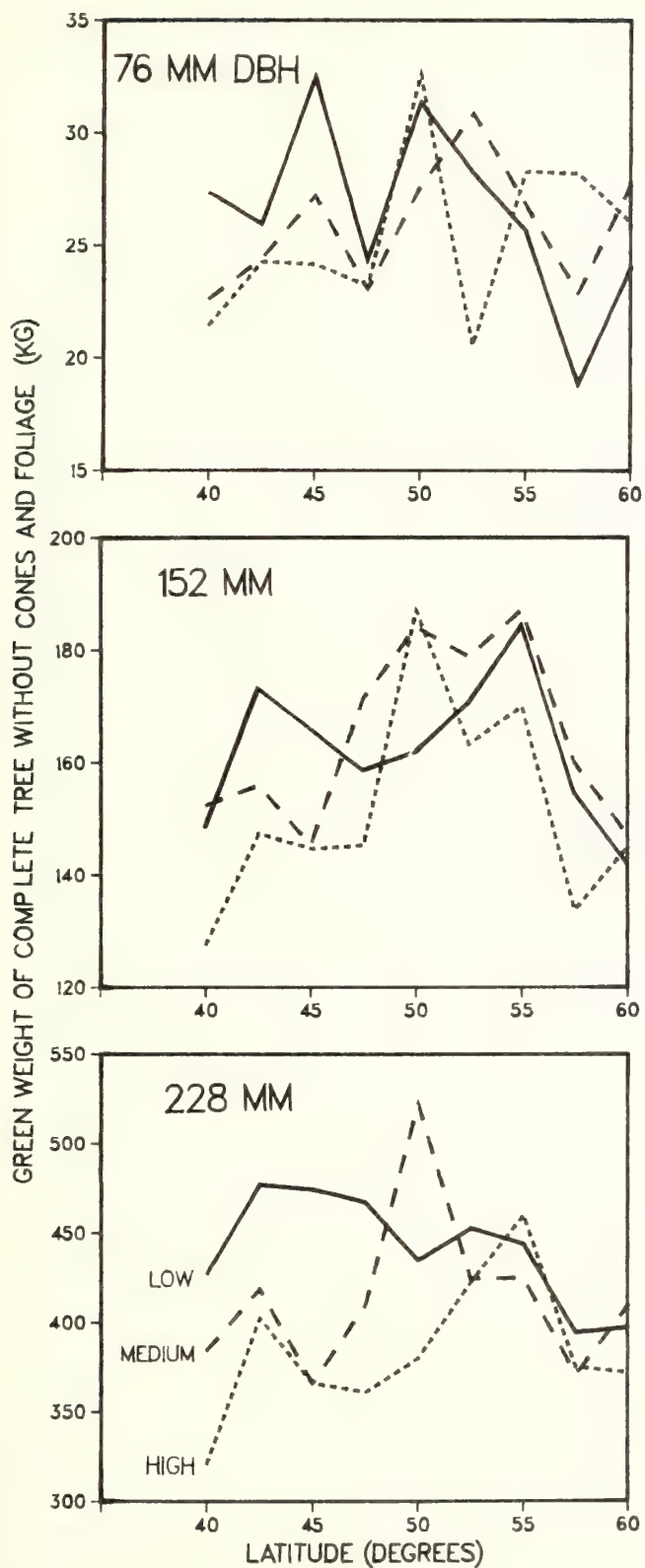


Figure 4-4—Green weight of foliage-free complete *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

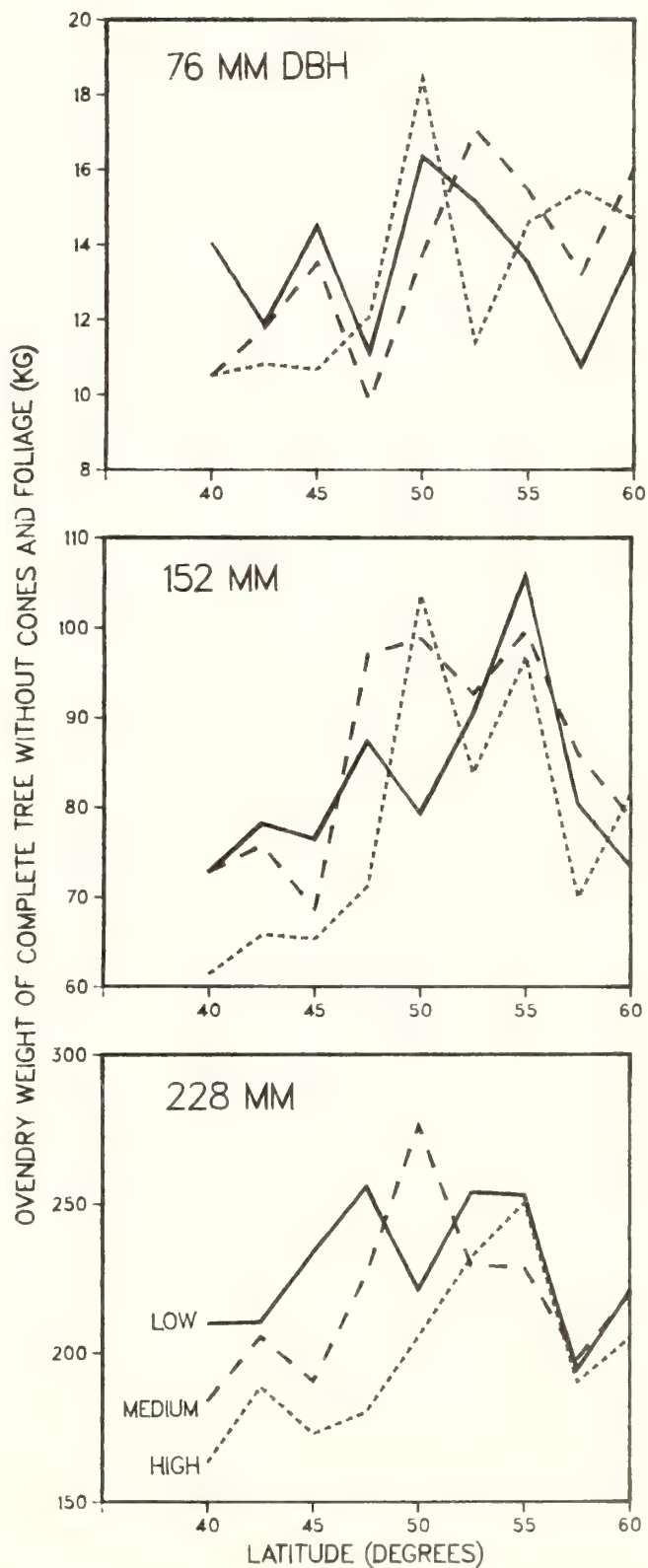


Figure 4-5—Ovendry weight of foliage-free complete *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

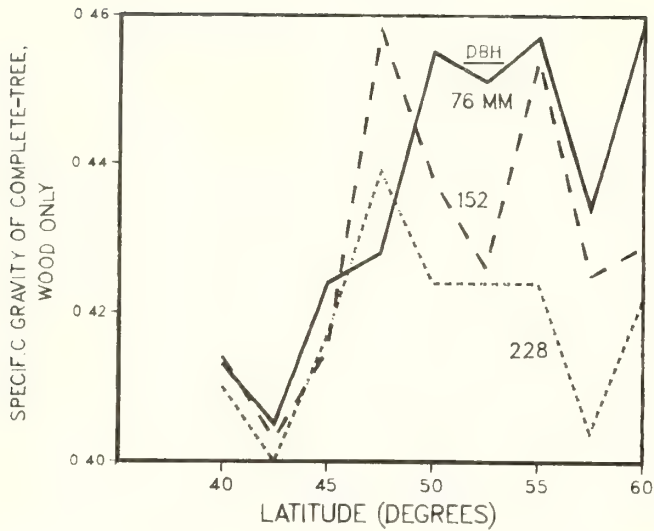


Figure 4-6—Specific gravity based on oven-dry weight and green volume of wood of complete *latifolia* trees of three diameters (including branches, stem, and stump-root system) related to latitude.

Complete Tree, Wood Only

Specific Gravity—Specific gravity of wood of the complete trees (branchwood, stemwood, and wood of the stump-root system) averaged 0.428, with standard deviation of 0.030, based on oven-dry weight and green volume. It was unrelated to elevational zone but was negatively correlated with d.b.h. (fig. 4-6), averaging 0.436 (0.035), 0.429 (0.027), and 0.418 (0.025) for trees 76, 152, and 228 mm in d.b.h.—a relationship unusual for conifers.

The relationship of treewood specific gravity to latitude (fig. 4-6) was the reverse of its moisture content (fig. 2-4). Treewood specific gravity averages were lowest (0.403) at 42.5 degrees latitude and increased with increasing latitude, reaching their highest levels in latitudes from 47.5 through 55 degrees (0.434 to 0.445) and at 60 degrees (0.436).

Weight, Green—On a green-weight basis, wood of branches, stem, and stump-root system of trees 76, 152, and 228 mm in d.b.h. averaged 21.88 (4.20), 141.11 (25.39), and 370.59 (60.15) kg. At most latitudes treewood weight was inversely correlated with elevational zone (fig. 4-7). Because of the interactions of treewood moisture content (fig. 2-4) and oven-dry weight (fig. 4-8) with latitude, strong latitudinal trends in treewood green weights were not evident.

Weight, Oven-dry—On an oven-dry-weight basis, however, treewood weight is positively correlated with latitude (fig. 4-8); with diameter data pooled it averaged minimum at 40 degrees (79.04 kg) and maximum at 55 degrees (107.56 kg). Trees in high-elevation zones—particularly those 228 mm in d.b.h.—tended to have less weight (oven-dry) of treewood than those in low or medium zones (fig. 4-8).

Treewood weights, oven-dry, for the three diameter classes averaged 11.41 (2.70), 72.55 (15.24), and 191.17 (32.93) kg.

LATIFOLIA

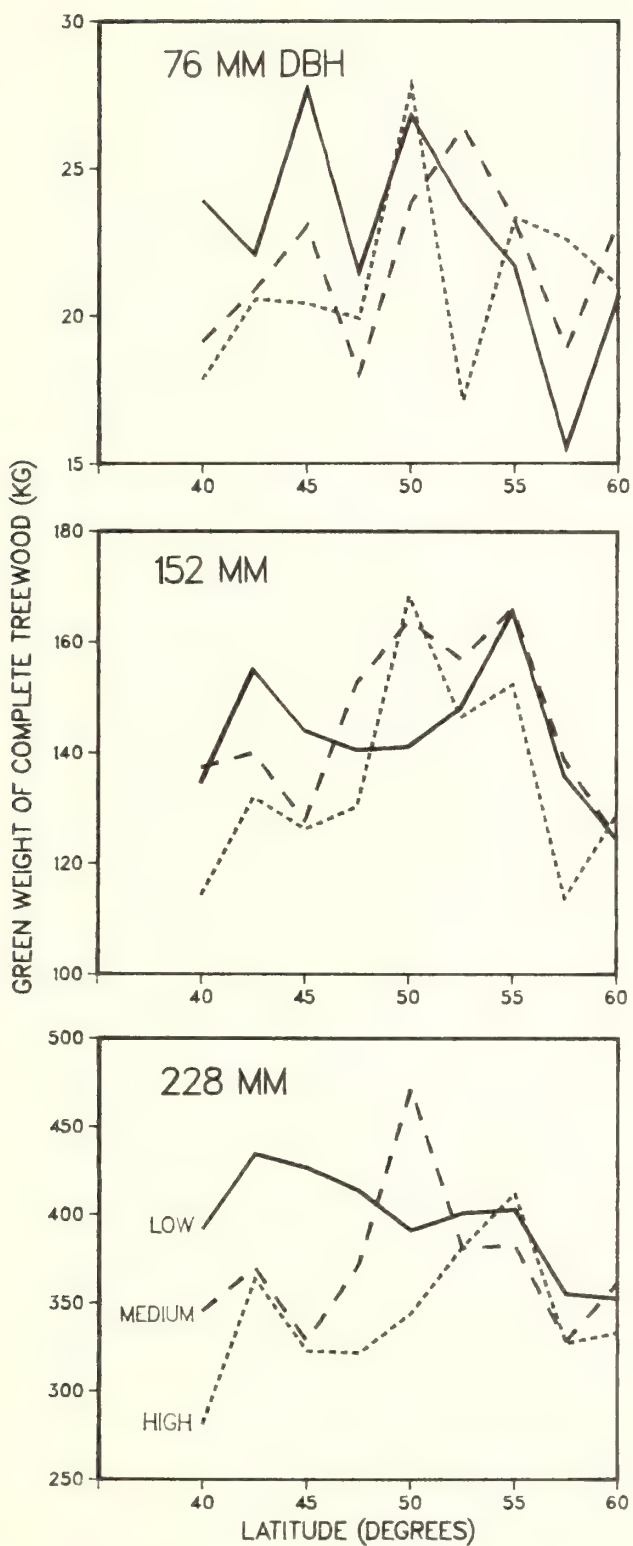


Figure 4-7—Green weight of wood of complete *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

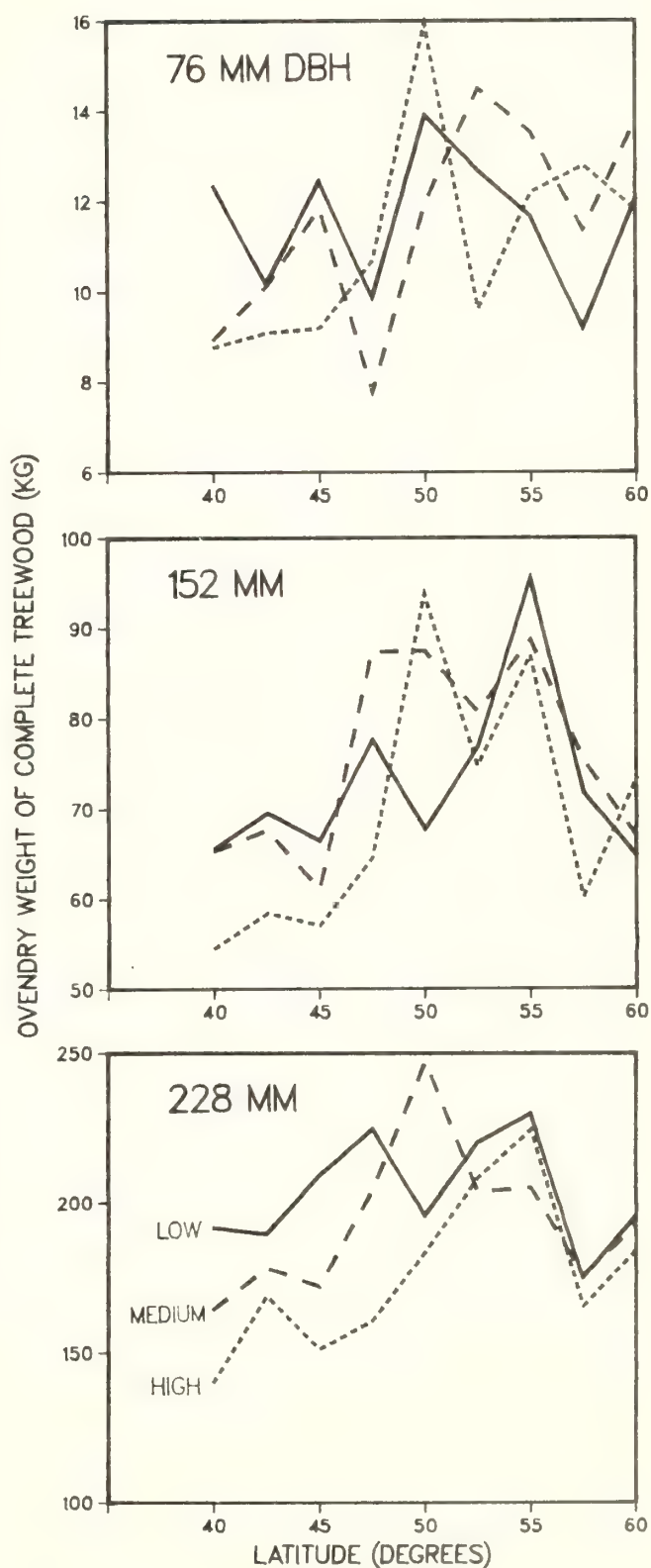


Figure 4-8—Oven dry weight of wood of complete *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

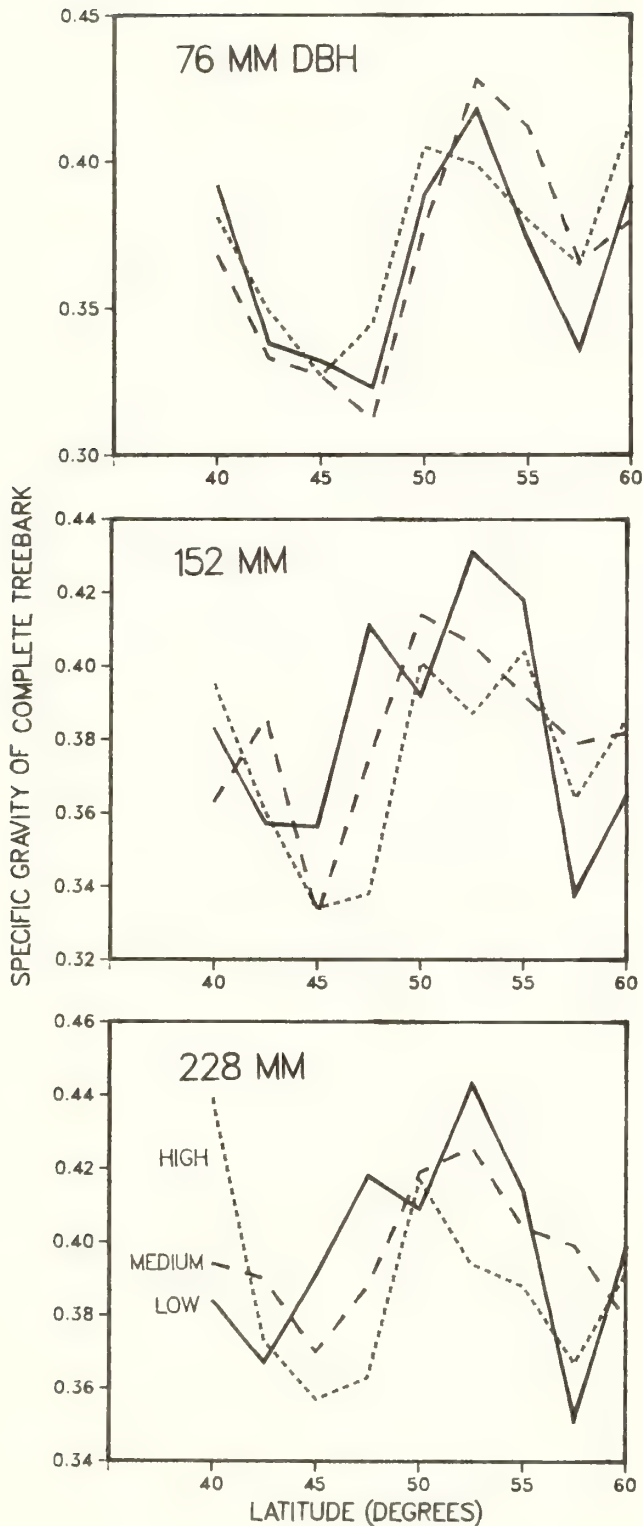


Figure 4-9—Specific gravity based on oven-dry weight and green volume of bark of complete *latifolia* trees of three diameters (including branches, stem, and stump-root system) related to latitude and elevational zone.

Complete Tree, Bark Only

Specific Gravity—Weighted-average specific gravity of bark from branches, stem, and stump-root system was positively correlated with d.b.h., averaging 0.369 (0.043), 0.380 (0.037), and 0.394 (0.035) for trees 76, 152, and 228 mm in d.b.h. Treebark specific gravity averaged least (0.347) at 45 degrees and most at 52.5 degrees latitude (0.415). Interactions between elevation and latitude were complex (fig. 4-9).

Overall average with diameter, latitudinal, and elevational data pooled was 0.381, with standard deviation of 0.040.

Weight, Green—Treebark green weight was positively correlated with d.b.h., averaging 3.91 (0.76), 17.34 (3.41), and 39.18 (6.78) kg for trees of the three diameter classes. Treebark weight was inversely correlated with elevational zone for trees 152 and 228 mm in d.b.h. (fig. 4-10), but pronounced latitudinal trends were not evident, except at 40 degrees, where treebark weight averaged less than at other latitudes.

Weight, Oven-dry—Similarly, oven-dry treebark weight averaged 1.84 (0.40), 8.69 (2.01), and 20.57 (4.14) kg for trees of the three diameter classes. For trees 152 and 228 mm in d.b.h., these weights were negatively correlated with elevational zone (fig. 4-11). Treebark weights, oven-dry, were lowest at 40 degrees latitude and highest at 52.5 degrees (fig. 4-11).

LATIFOLIA

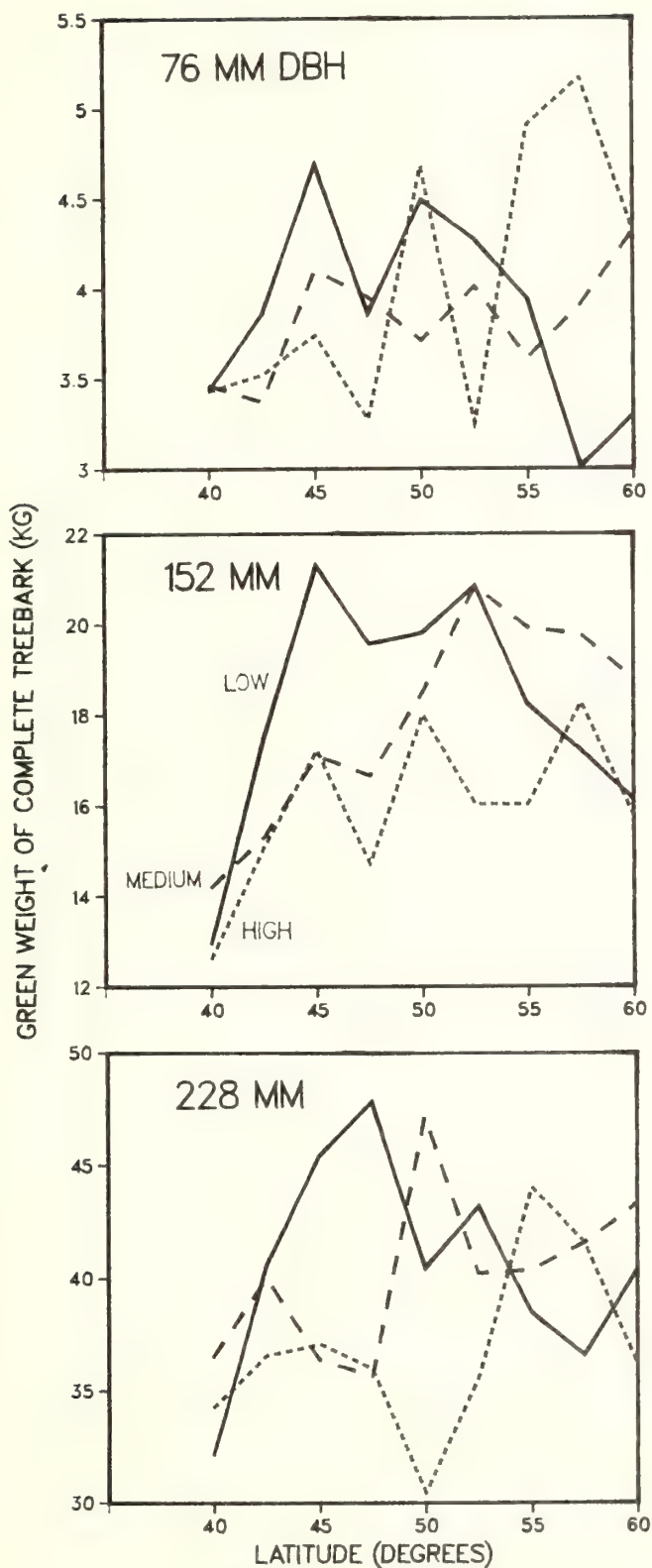


Figure 4-10—Green weight of bark of complete *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

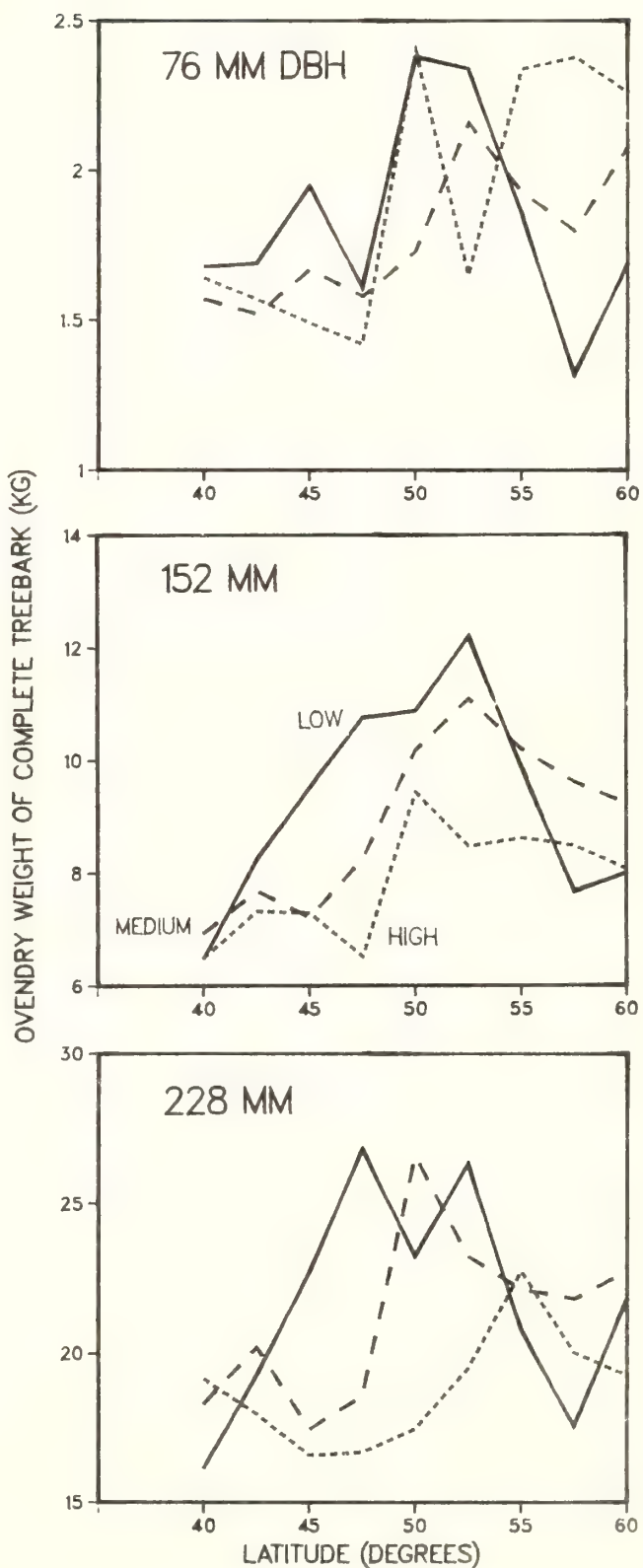


Figure 4-11—Ovendry weight of bark of complete *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

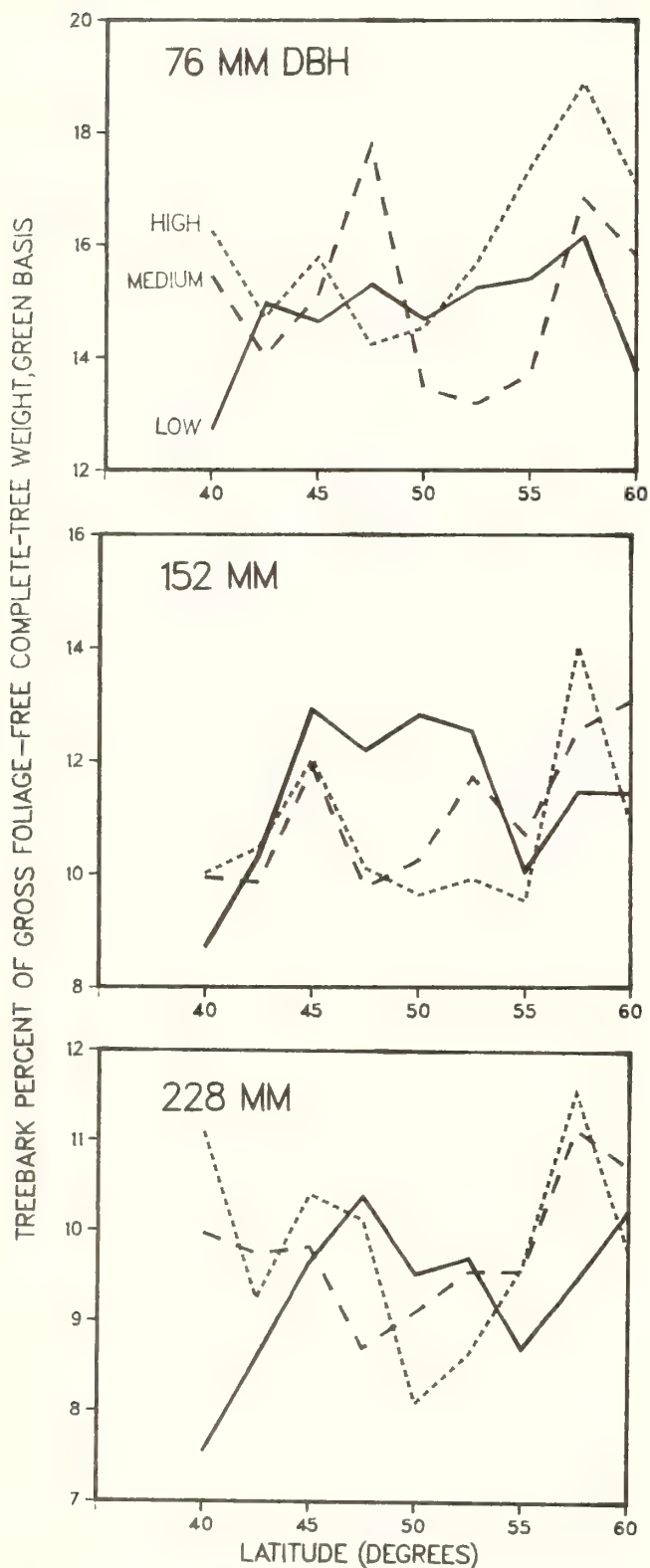


Figure 4-12—Treebark as percentage of gross foliage-free complete-tree weight (green basis) for *latifolia* trees of three diameters related to latitude and elevational zone.

LATIFOLIA

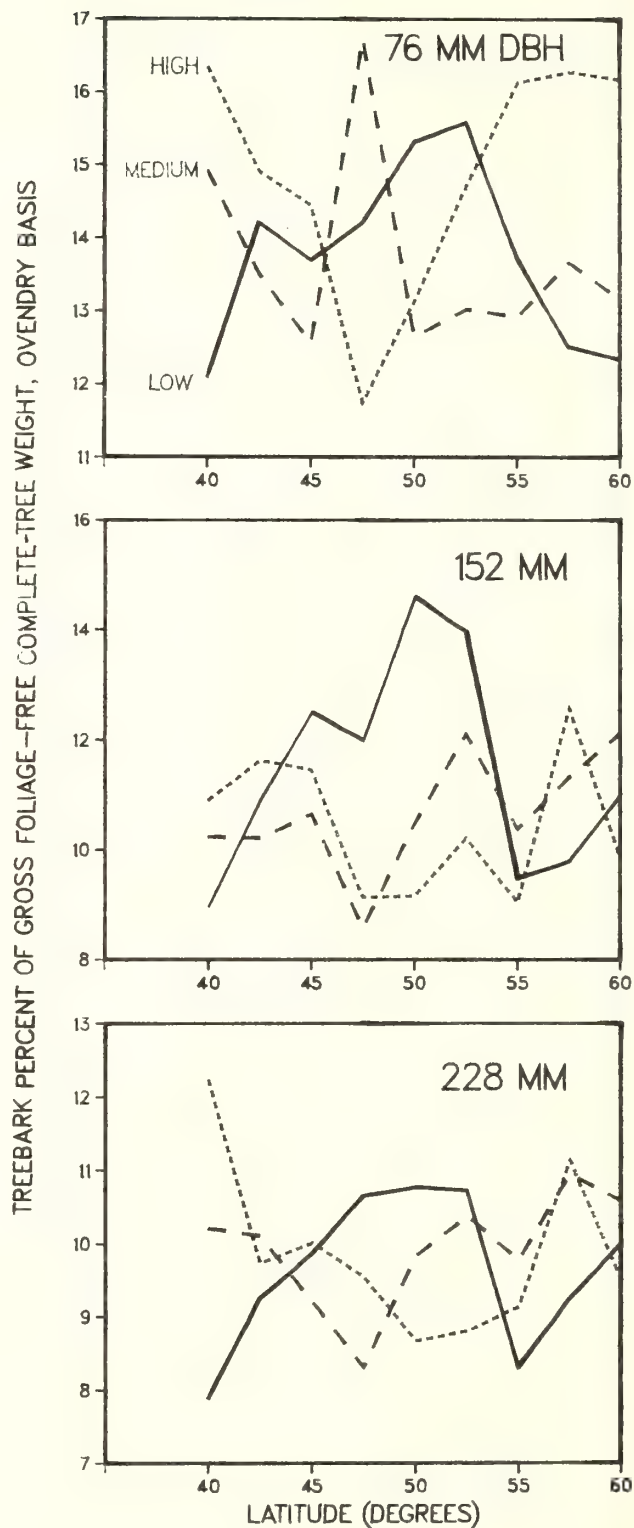


Figure 4-13—Treebark as percentage of gross foliage-free complete-tree weight (ovendry basis) for *latifolia* trees of three diameters related to latitude and elevational zone.

Percentage of Weight of Gross Foliage-Free Complete Tree, Green and Ovendry—With all diameter, latitudinal, and elevational data pooled, treebark averaged 12.00 (3.08) percent of foliage-free complete-tree green weight, and 11.59 (2.80) percent on an ovendry weight basis. The percentages were negatively correlated with d.b.h., as follows:

D.b.h.	Green	Ovendry
mm	Percent	
76	15.28 (2.23)	14.10 (2.32)
152	11.06 (1.99)	10.86 (2.29)
228	9.66 (1.54)	9.81 (1.72)

Elevational and latitudinal trends in treebark weight percent were not pronounced, and interactions were complex (figs. 4-12 and 4-13).

Foliage

Here and elsewhere in this text the term “foliage” means “technical foliage”; that is, all needles and needle-bearing twigs up to 6-mm diameter outside bark.

Weight, Green—Green foliage weight was unrelated to latitude and elevational zone, but was positively correlated with d.b.h., averaging 2.47 (1.33), 11.05 (4.74), and 26.71 (10.27) kg for trees 76, 152, and 228 mm in d.b.h.—a relationship approximately linear with d.b.h.².

Weight, Ovendry—Similarly, ovendry foliage weight was not significantly related to latitude or elevational zone, but was positively correlated with d.b.h., averaging 1.14 (0.59), 5.28 (2.22), and 12.90 (4.58) kg for trees of the three diameter classes.

Tree Component Proportion, Green-Weight Basis—Foliage green weight averaged 7.13 percent of green complete-tree weight, with standard deviation of 3.52 percentage points. It was unrelated to elevational zone, but was negatively correlated with d.b.h., averaging 8.68 (4.40), 6.58 (2.96), and 6.14 (2.40) percent for trees 76, 152, and 228 mm in d.b.h.

Foliage as a percentage of green weight was negatively correlated with latitude (fig. 4-14); averages were highest at the southernmost latitude of 40 degrees (8.57 percent) and were lowest at 52.5 degrees (5.40 percent).

Tree Component Proportion, Ovendry-Weight Basis—Similarly, foliage ovendry weight averaged 6.80 percent of ovendry complete-tree weight, with standard deviation of 3.66 percentage points. It was unrelated to elevational zone, but was negatively correlated with d.b.h., averaging 8.25 (4.70), 6.32 (3.13), and 5.82 (2.33) percent for trees 76, 152, and 228 mm in d.b.h.

Foliage as a percentage of ovendry weight was negatively correlated with latitude (fig. 4-15); averages were highest (8.37 percent) in the two southernmost latitudes and lowest (5.06 percent) at 52.5 degrees.

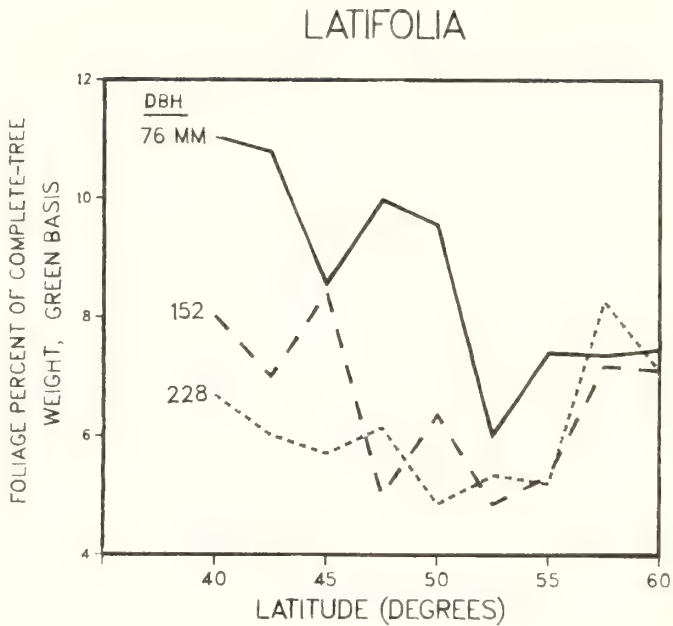


Figure 4-14—Foliage as percentage of complete-tree weight (green basis) for *latifolia* trees of three diameters related to latitude.

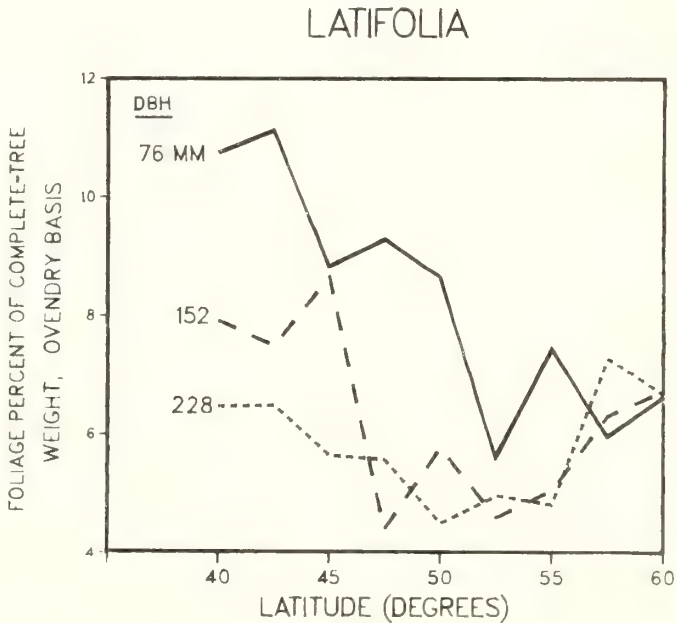


Figure 4-15—Foliage as percentage of complete-tree weight (ovendry basis) for *latifolia* trees of three diameters related to latitude.

Cones, Individual

Weight, Green—With all data pooled, green cones sampled from the tip 305 mm of the top 25 branches had average weight of 6.2 g, with standard deviation of 2.6 g. Green-cone weight was positively correlated with d.b.h., averaging 5.2 (2.4), 6.0 (2.2), and 6.8 (2.8) g for trees 76, 152, and 228 mm in d.b.h. Elevational trends varied with latitude (fig. 4-16); cones weighed least at 45 degrees latitude (4.3 g) and most at latitudes 52.5 and 60 degrees (7.8 g). In some of the southern latitudes, none of the 76-mm trees had cones on the top 25 branches, so cone weights could not be determined (fig. 4-16).

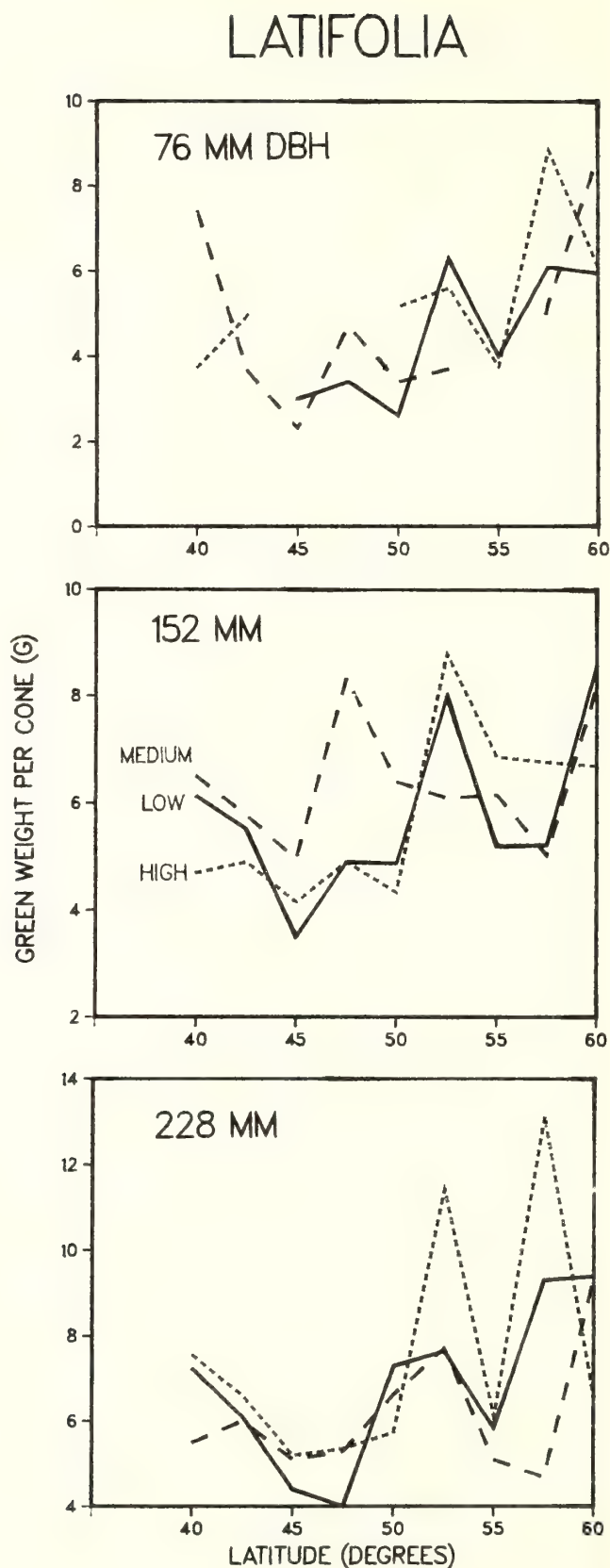


Figure 4-16—Green weight of individual cones from the tip 305 mm of the top 25 branches of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—On an ovendry-weight basis, cone weight was positively correlated with latitude (fig. 4-17); interactions of latitude and elevation were complex.

With all data pooled, cones had an average ovendry weight of 5.0 g, with standard deviation of 2.1 g. Cone weight, ovendry, was positively correlated with d.b.h., averaging 4.2 (2.0), 4.8 (1.8), and 5.6 (2.2) g for trees of the three diameter classes.

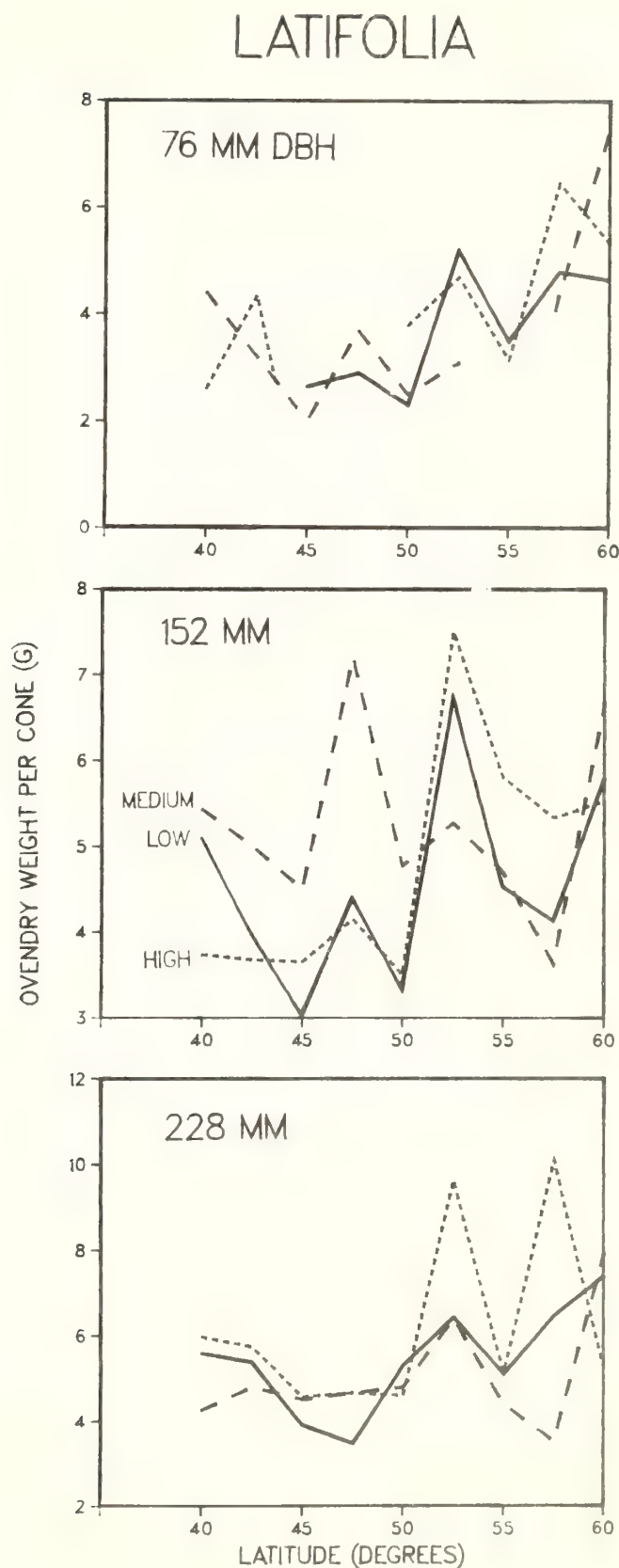


Figure 4-17—Ovendry weight of individual cones from the tip 305 mm of the top 25 branches of *latifolia* trees of three diameters related to latitude and elevational zone.

All Cones on Tree

As explained in chapter 1, weight of all cones on each tree was computed (based on the number of cones counted on the tip 305 mm of the top 25 branches), not measured directly, and therefore results should be interpreted with caution.

Weight, Green—Green weight of all cones on each tree was unrelated to latitude and elevational zone, but was positively correlated with d.b.h., averaging 0.14 (0.32), 0.96 (1.02), and 3.74 (3.62) kg for trees of the three diameter classes.

Weight, Ovendry—Similarly, ovendry weight of all cones per tree averaged 0.11 (0.27), 0.78 (0.83), and 3.09 (3.09) kg for trees of the three diameter classes.

Tree Component Proportion, Green-Weight Basis—Green-cone percentage of complete green-tree weight averaged 0.62 percent, with standard deviation of 0.86 percentage points. It was not significantly related to elevational zone but averaged 0.53, 0.61, and 0.75 percent in low, medium, and high zones. Green-cone weight proportion was positively correlated with d.b.h., averaging 0.46 (1.03), 0.57 (0.61), and 0.86 (0.85) percent for trees 76, 152, and 228 mm in d.b.h.

Green-cone weight proportion tended to increase slightly with increasing latitude (fig. 4-18, top), with minimum average weight proportion (0.37 percent) at 47.5 degrees and maximum of 1.03 percent at 60 degrees.

Tree Component Proportion, Ovendry-Weight Basis—On an ovendry basis, cone weight proportion averaged 1.00 percent of complete-tree weight, with standard deviation of 1.34 percentage points. Although the differences with elevational zone were not significant, the average weight proportions for low, medium, and high zones were 0.82, 0.96, and 1.21 percent.

Ovendry cone-weight proportions did not vary significantly with latitude (fig. 4-18, bottom), but were positively correlated with d.b.h., averaging 0.73 (1.62), 0.90 (0.95), and 1.37 (1.39) percent for trees of the three diameter classes.

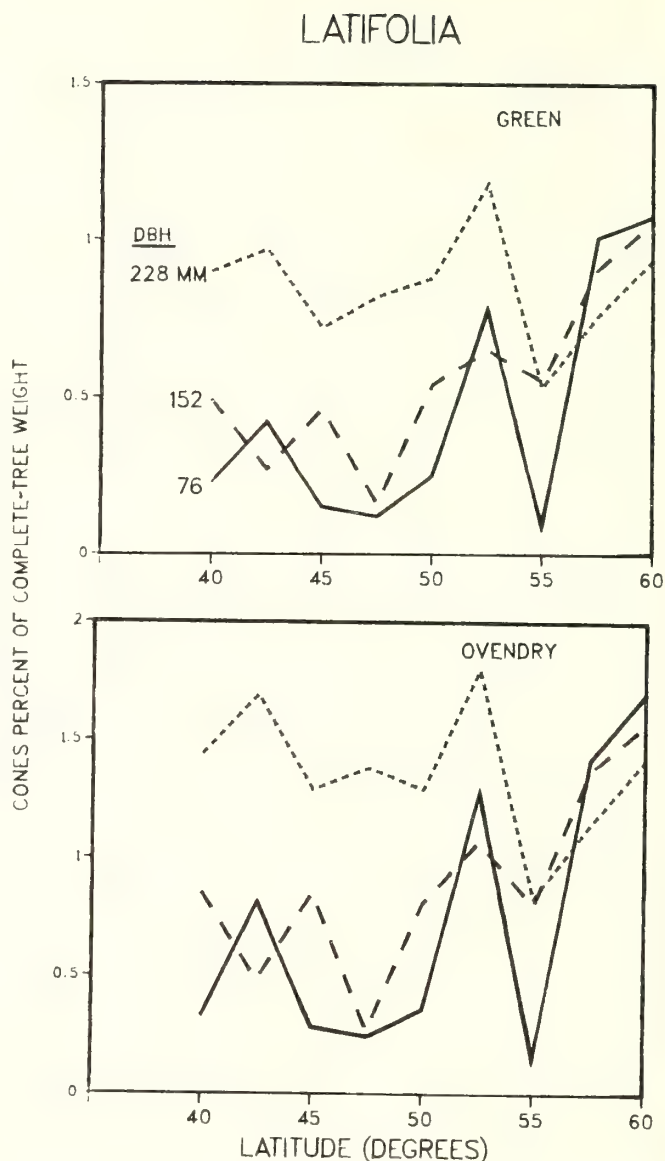


Figure 4-18—Cones as percentage of complete-tree weight (green and ovendry) of *latifolia* trees of three diameters related to latitude.

Dead Branchwood

Weight, Green—Green weight of dead branches was positively correlated with d.b.h., averaging 0.32 (0.25), 2.03 (2.00), and 5.76 (5.41) kg for trees 76, 152, and 228 mm in d.b.h. Trees from high-elevation zones retained less weight of dead branches than those from medium and low zones (fig. 4-19); with diameter and latitudinal data pooled, averages were 1.92, 2.77, and 3.41 kg from the three zones, respectively. Also, trees in southern latitudes retained less weight of dead branches than those in northern latitudes; this relationship was most pronounced in the smaller trees (fig. 4-19).

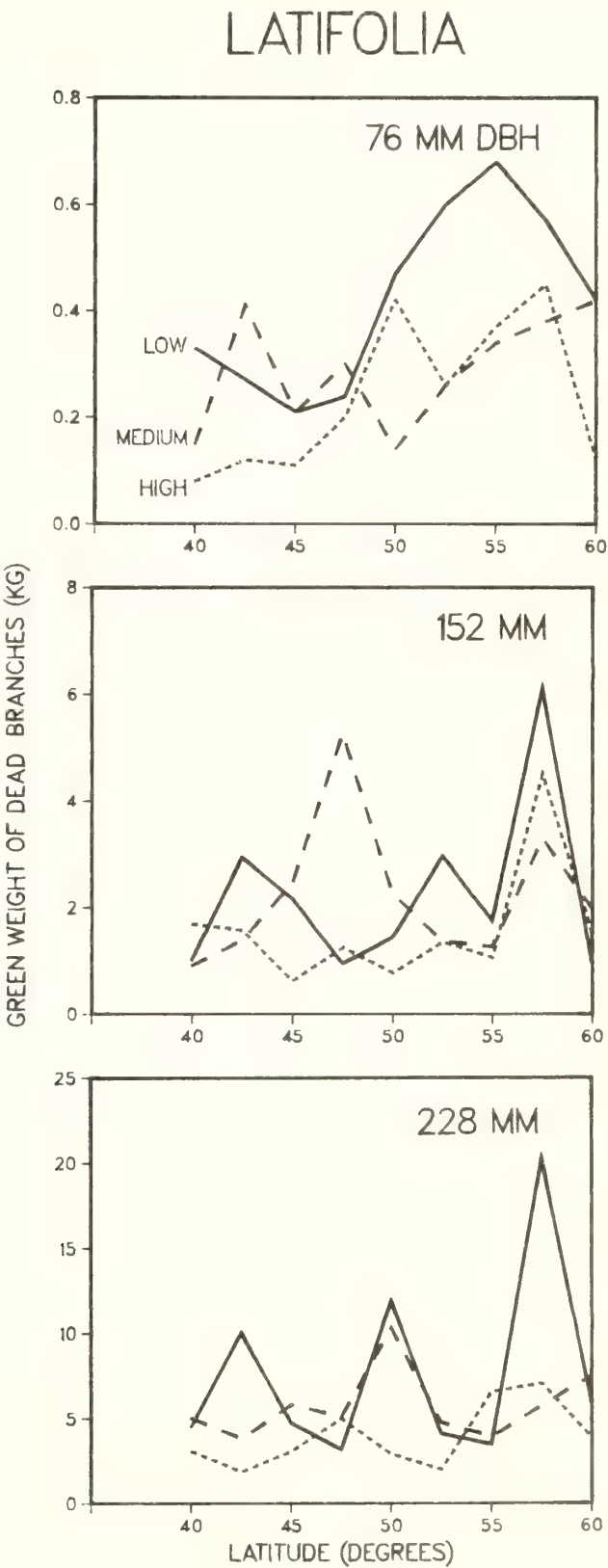


Figure 4-19—Green weight of dead branches from *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis (fig. 4-20), latitudinal and elevational trends were similar to those for green dead branches. With diameter and latitudinal data pooled, trees from high-, medium-, and low-elevation zones retained 1.58, 2.34, and 2.86 kg of dead branches, respectively.

Ovendry weight of dead branches was positively correlated with d.b.h., averaging 0.26 (0.21), 1.65 (1.41), and 4.87 (4.46) kg for trees of the three diameter classes.

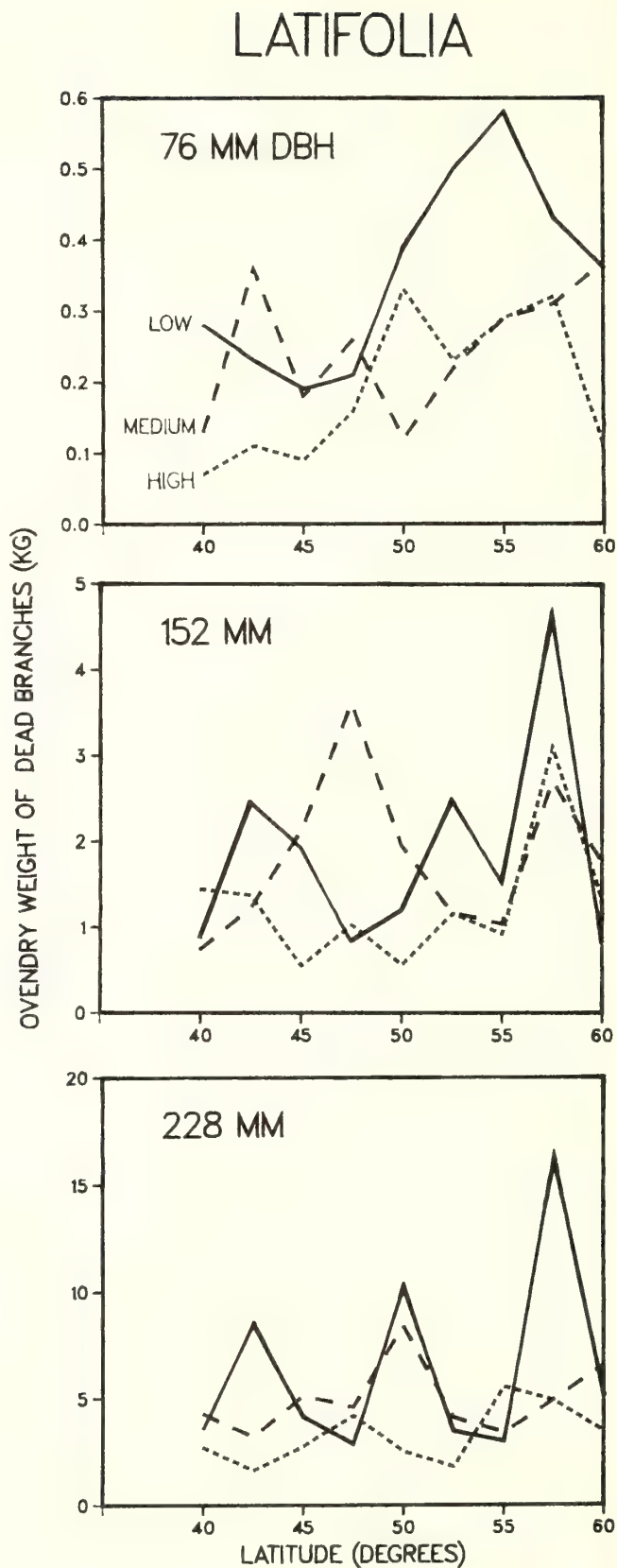


Figure 4-20—Ovendry weight of dead branches of *latifolia* trees of three diameters related to latitude and elevational zone.

Tree Component Proportion, Green-Weight Basis—On a green-weight basis, dead branches comprised 1.23 percent of complete-tree weight (including foliage), with standard deviation of 1.13 percentage points. This weight proportion was unrelated to d.b.h., but in most latitudes (fig. 4-21) trees from low-elevation zones had a greater weight proportion of dead branches than those in high zones; averages for low, medium, and high zones were 1.51, 1.21, and 0.97 percent. Trees in northern latitudes tended to have a greater weight proportion of dead branches than those in the south (fig. 4-21).

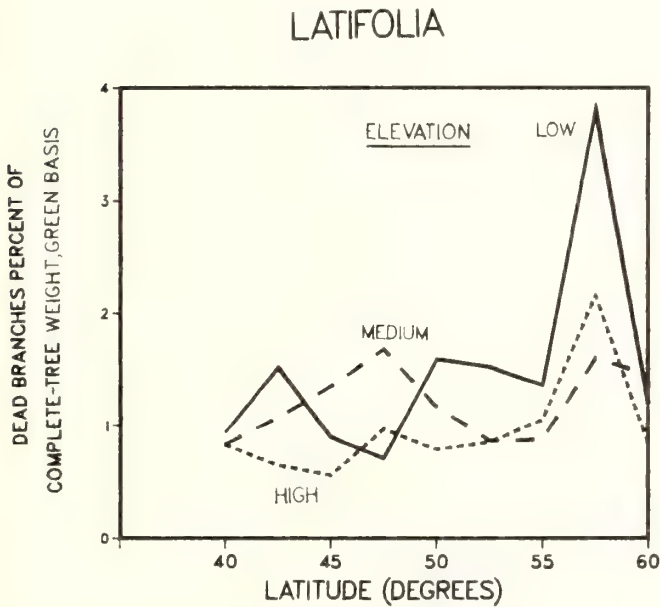


Figure 4-21—Dead branches as percentage of weight of complete *latifolia* trees with foliage (green basis) related to latitude and elevational zone.

Tree Component Proportion, Ovendry-Weight Basis—On an ovendry-weight basis, dead branches averaged 1.98 percent of complete-tree weight including foliage, with standard deviation of 1.72 percentage points. The proportion was unrelated to d.b.h., but negatively correlated with elevational zone in most latitudes (fig. 4-22), averaging 2.44, 1.98, and 1.53 percent in low-, medium-, and high-elevation zones.

Dead branchwood ovendry-weight proportion averaged least (1.47 percent) in the southernmost latitude of 40 degrees and most (3.73 percent) at 57.5 degrees (fig. 4-22).

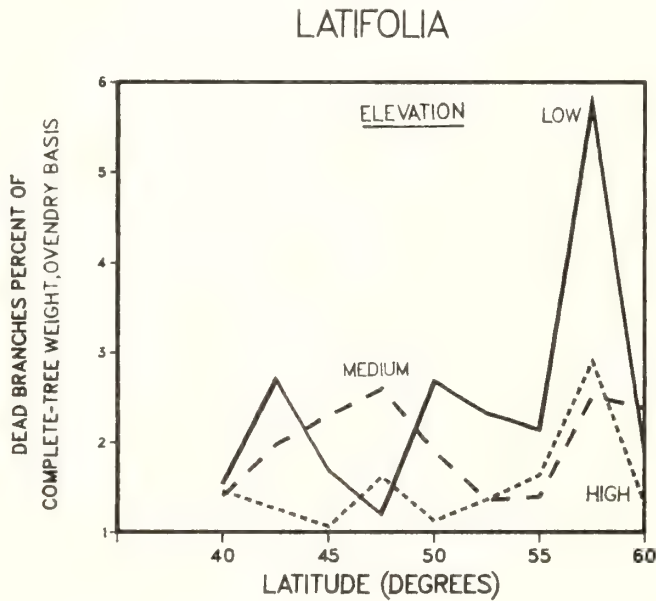


Figure 4-22—Dead branches as percentage of weight of complete *latifolia* trees with foliage (ovendry basis) related to latitude and elevational zone.

Live Branches, Wood Plus Bark

Specific Gravity Specific gravity of wood plus bark of live branches averaged 0.457, with standard deviation of 0.031, based on oven-dry weight and green volume. It was unrelated to either d.b.h. or elevational zone.

Its latitudinal variation (fig. 4-23) was inverse to the latitudinal variation of the moisture content of this tree portion (fig. 2-9). Wood-plus-bark specific gravity averaged least (0.439) at 45 degrees latitude and most (0.477) at 52.5 degrees (fig. 4-23).

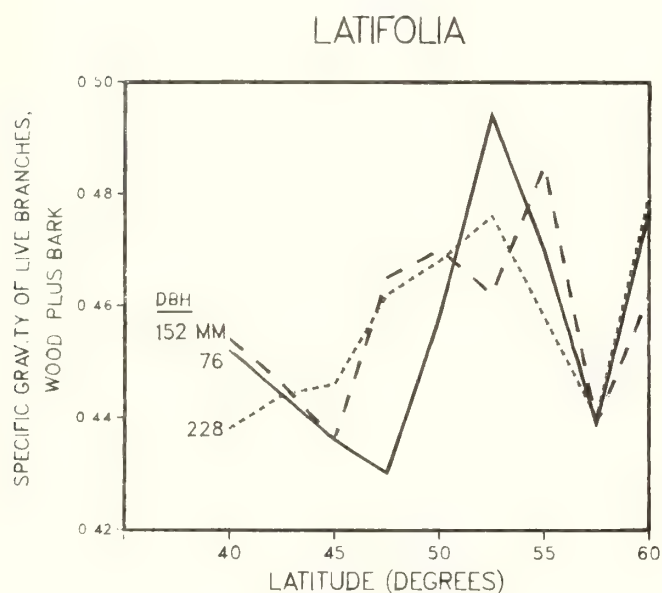


Figure 4-23—Specific gravity of wood plus bark of live branches (based on oven-dry weight and green volume) of *latifolia* trees of three diameters related to latitude

Weight, Green—Green weight of foliage-free live branches, wood plus bark, was positively correlated with d.b.h., averaging 1.32 (0.74), 9.08 (4.00), and 31.92 (13.80) kg for trees 76, 152, and 228 mm in d.b.h. Trees in high-elevation zones tended to have less weight of green branches than those in low zones, but latitudinal trends were not pronounced (fig. 4-24).

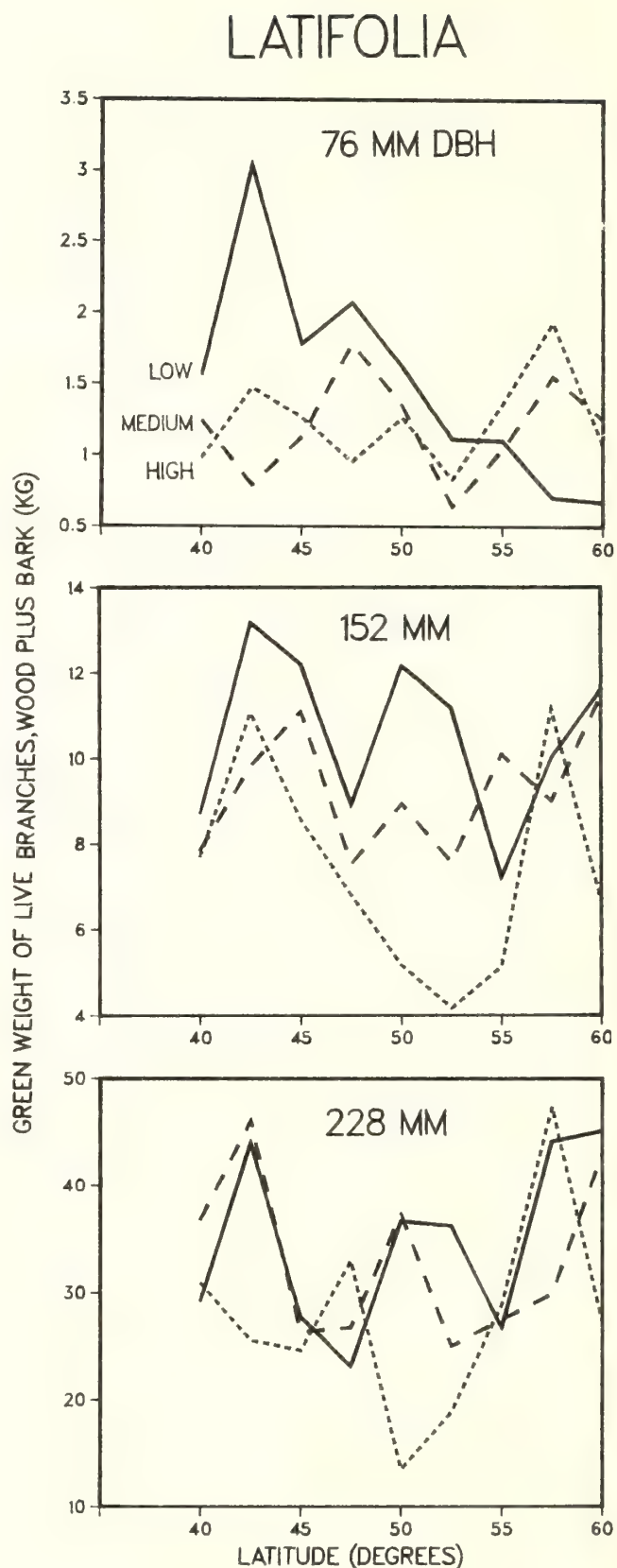


Figure 4-24—Green weight of wood plus bark of live branches of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—Similarly, ovendry weight of live branches averaged 0.67 (0.35), 4.62 (1.93), and 16.32 (6.79) kg for trees of the three diameter classes, with no prominent latitudinal trends (fig. 4-25). Branch weights were negatively correlated with elevational zone, averaging (with diameter data pooled) 7.91, 7.46, and 6.23 kg for trees in low-, medium-, and high-elevation zones, respectively.

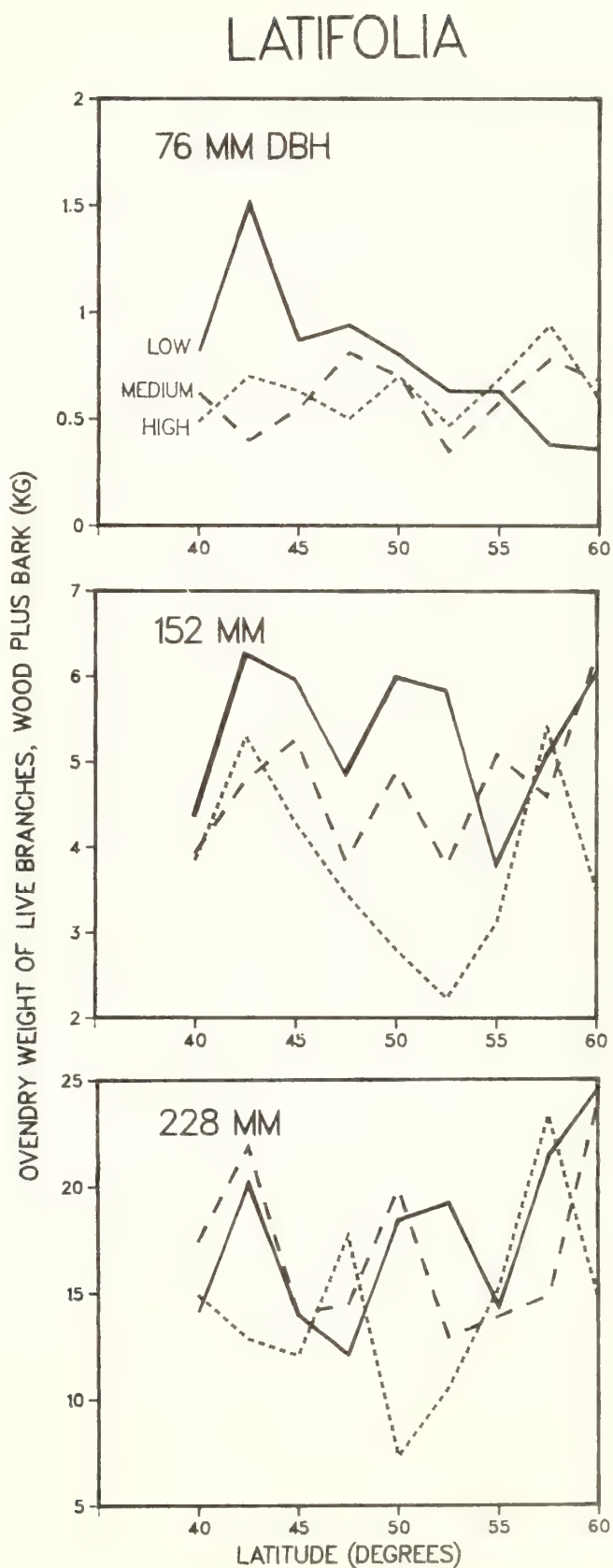


Figure 4-25—Ovendry weight of wood plus bark of live branches of *latifolia* trees of three diameters related to latitude and elevational zone

Green Weight to Yield 1 m³ of Wood—Weight of foliage-free green live branches required to yield 1 m³ of wood averaged 1,448 kg, with standard deviation of 209 kg. This weight requirement was unrelated to elevational zone, but was negatively correlated with d.b.h., averaging 1,649 (162), 1,427 (134), and 1,267 (116) kg for trees 76, 152, and 228 mm in d.b.h. The requirement varied somewhat with latitude; it averaged maximum (1,543 kg) at 45 degrees and minimum (1,411 kg) at 47.5 degrees (fig. 4-26).

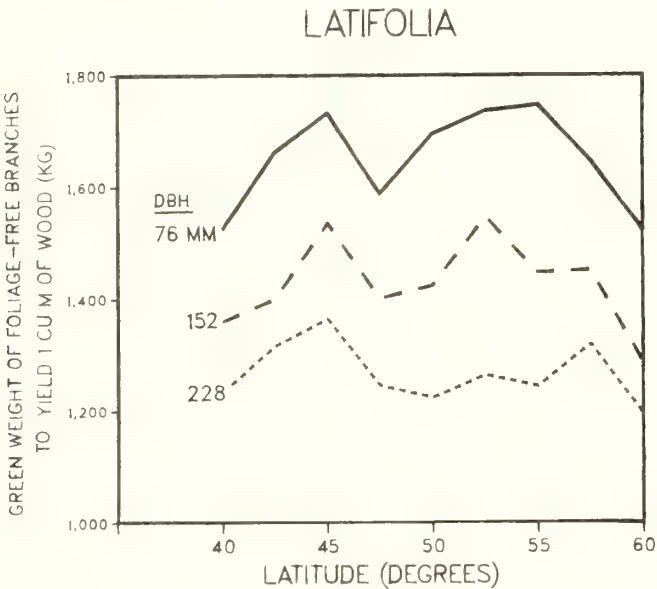


Figure 4-26—Weight of green foliage-free live branches to yield 1 m³ of bark-free wood from *latifolia* trees of three diameters related to latitude.

Tree Component Proportion, Green-Weight Basis—

With all data pooled, green, foliage-free live branches averaged 5.80 percent of complete-tree green weight including foliage, with standard deviation of 2.95 percentage points. This proportion was positively correlated with d.b.h., averaging 4.64 (2.55), 5.40 (2.43), and 7.35 (3.15) percent for trees 76, 152, and 228 mm in d.b.h. Latitudinal trends were not pronounced, but trees in high-elevation zones tended to have less percentage of their green weight in live branches than those in low zones (fig. 4-27). With diameter and latitudinal data pooled, trees in high, medium, and low zones averaged 5.31, 5.76, and 6.32 percent.

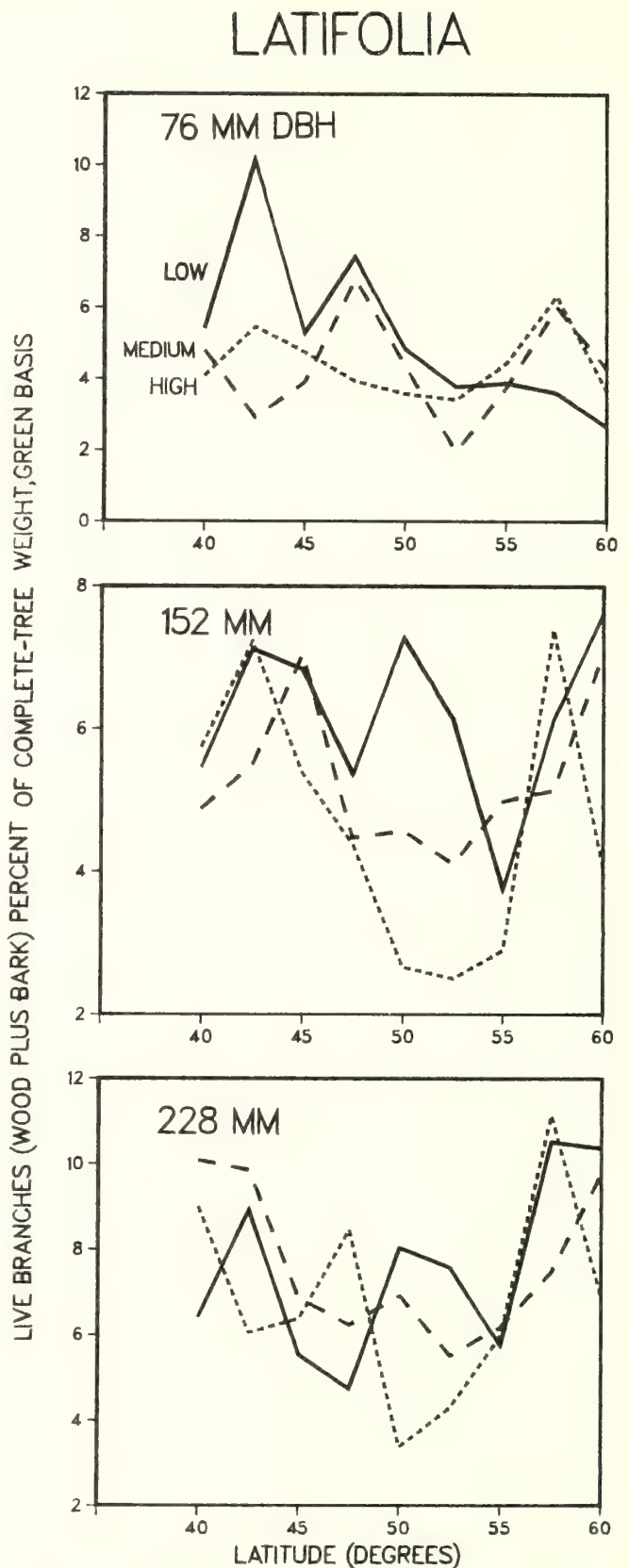


Figure 4-27—Live branches, wood plus bark but not foliage, as percentage of complete-tree green weight—including foliage, for *latifolia* trees of three diameters related to latitude and elevational zone.

Tree Component Proportion, Ovendry-Weight Basis— Ovendry, foliage-free live branches averaged 5.88 percent of ovendry complete-tree weight including foliage, with standard deviation of 3.02 percentage points. This percentage was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 4.81 (2.68), 5.49 (2.61), and 7.32 (3.19) percent for trees of the three diameter classes. As a percentage of total ovendry tree weight, weight of live branches was lowest in the middle latitudes (4.38 percent at 52.5 degrees) and highest (7.37 percent) at 42.5 degrees (fig. 4-28).

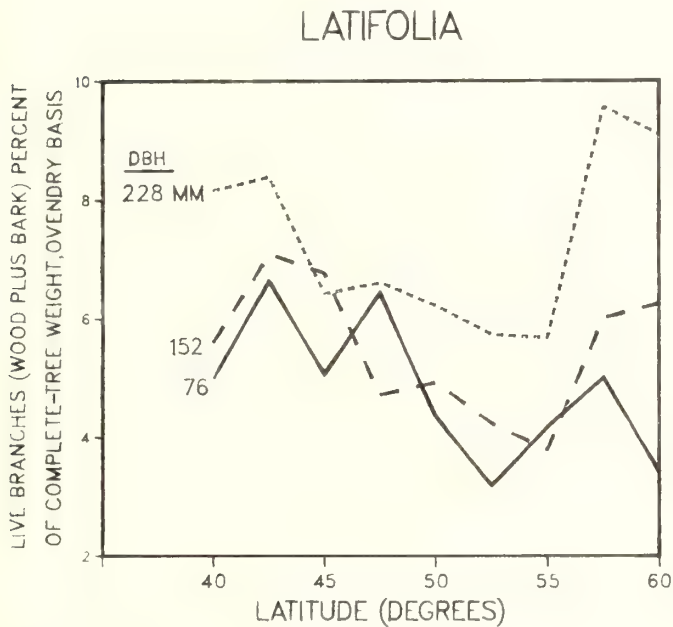


Figure 4-28—Live branches, wood plus bark but not foliage, as percentage of complete-tree ovendry weight—including foliage, for *latifolia* trees of three diameters related to latitude.

Live Branchwood

Specific Gravity—Wood of live branches had the highest specific gravity of any tree component (table 4-2), averaging 0.487, with standard deviation of 0.036, based on ovendry weight and green volume. It was unrelated to elevational zone, but was negatively correlated with d.b.h., averaging 0.499 (0.041), 0.487 (0.032), and 0.477 (0.030) for trees 76, 152, and 228 mm in d.b.h.

Latitudinal relationship to branchwood specific gravity (fig. 4-29) was inverse to that of moisture content (fig. 2-10). Average specific gravity of branchwood was lowest (0.463) in the southernmost latitude of 40 degrees and increased to an average range from 0.484 to 0.502 in latitudes 45 through 60 degrees (fig. 4-29).

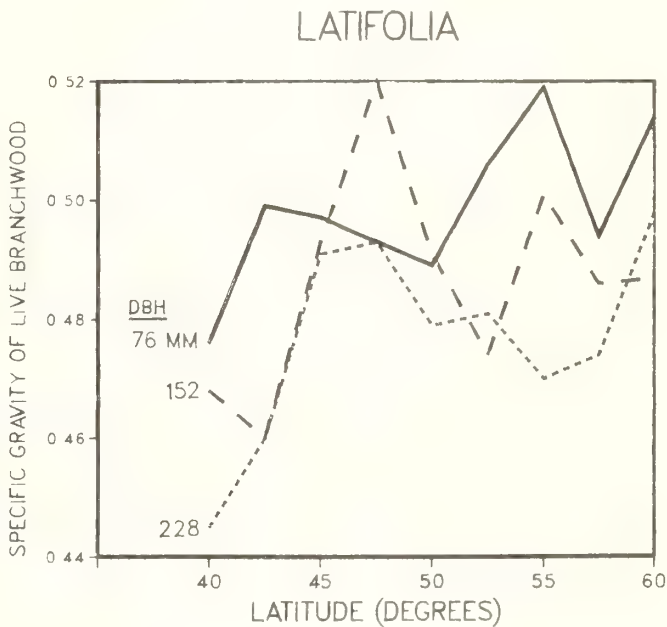


Figure 4-29—Specific gravity of live branchwood (based on ovendry weight and green volume) of *latifolia* trees of three diameters related to latitude.

Weight, Green—Weight of green live branchwood was positively correlated with d.b.h., averaging 0.74 (0.45), 5.93 (2.71), and 23.14 (10.55) kg for trees of the three diameter classes. In small-diameter trees, but not in large, branchwood weight was less in northern than in southern latitudes (fig. 4-30). Also, green branchwood weight was inversely correlated with elevational zone, averaging—with diameter data pooled—11.16, 10.27, and 8.39 kg for trees in low, medium, and high zones.

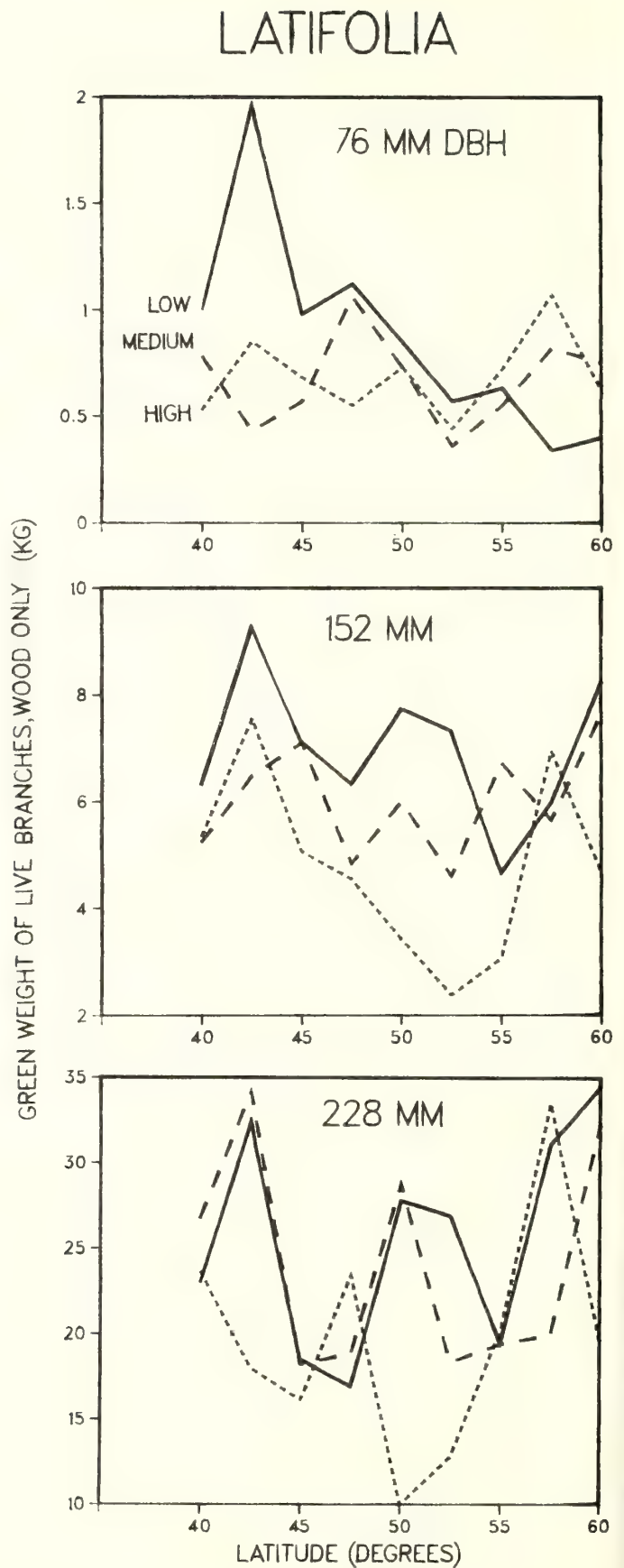


Figure 4-30—Green weight of wood of live branches of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—Ovendry weight of wood of live branches also varied inversely with elevational zone, averaging—with diameter data pooled—5.76, 5.38, and 4.45 kg in low, medium, and high zones (fig. 4-31). In low elevational zones, 76-mm trees had less branchwood weight in northern latitudes than in southern. All diameters considered, branchwood weight was least at 52.5 degrees (4.26 kg) and most at 60 degrees (6.78 kg); but trends were complex (fig. 4-31).

Weight of ovendry branchwood was positively correlated with d.b.h., averaging 0.40 (0.22), 3.11 (1.38), and 12.09 (5.34) kg for trees 76, 152, and 228 mm in d.b.h.

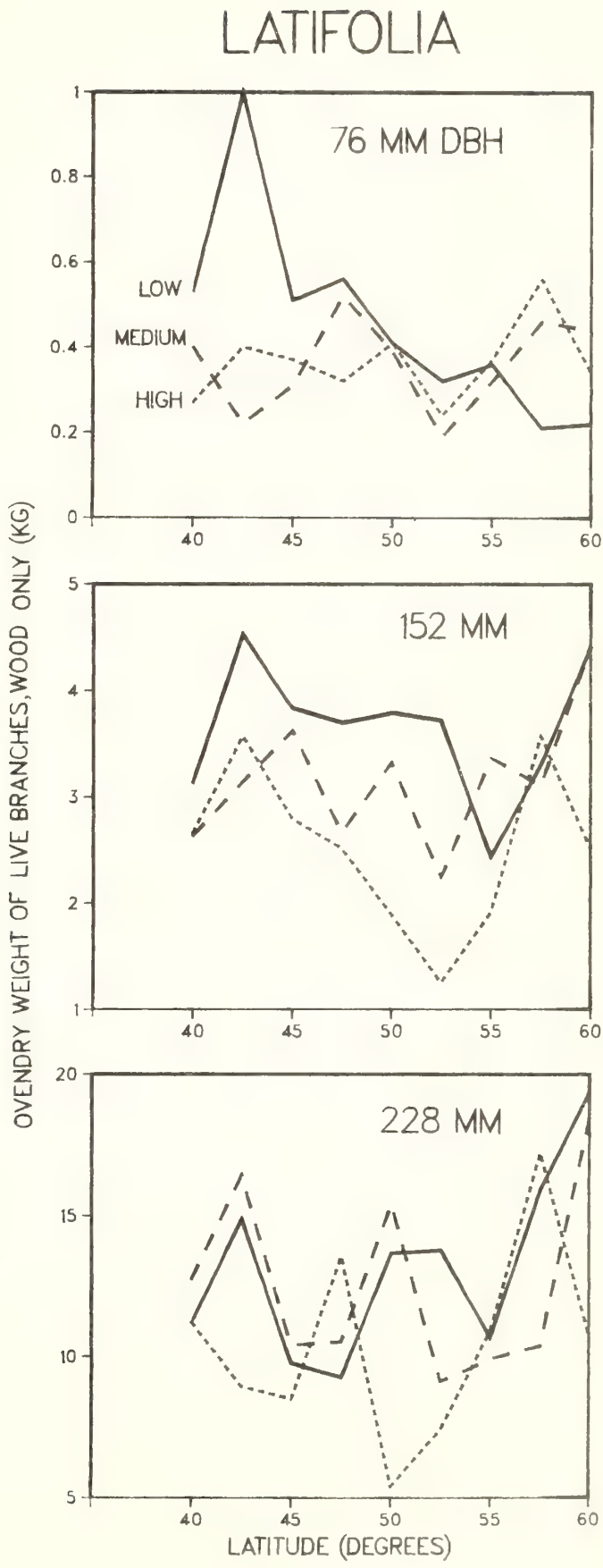


Figure 4-31—Ovendry weight of wood of live branches of *latifolia* trees of three diameters related to latitude and elevational zone.

Live Branchbark

Specific Gravity—The bark of live branches had average specific gravity of 0.410, with standard deviation of 0.051. This specific gravity was unrelated to either d.b.h. or elevational zone. It did, however, vary significantly with latitude (fig. 4-32), averaging minimum (0.365) at 45 degrees and maximum (0.466) at 52.5 degrees.

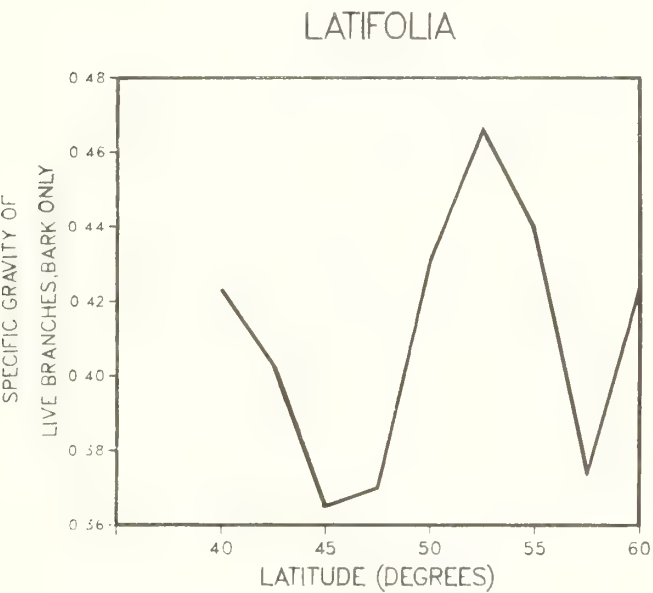


Figure 4-32—Specific gravity of bark of live branches (based on oven-dry weight and green volume) of *latifolia* trees related to latitude.

Weight, Green—Green weight of bark of live branches was positively correlated with d.b.h., averaging 0.57 (0.32), 3.14 (1.44), and 8.80 (3.66) kg for trees of the three diameter classes. Branchbark weight of low-elevation 76-mm trees was less in the north than in the south, but the reverse was true for 228-mm trees in low-elevation zones (fig. 4-33). Trees of 152-mm d.b.h. in high-elevation zones had less green weight of branchbark than those in lower zones (fig. 4-33).

Weight, Oven-dry—Oven-dry weight of live branchbark was unrelated to latitude, but was positively correlated with d.b.h., averaging 0.28 (0.14), 1.51 (0.64), and 4.23 (1.65) kg for trees of the three diameters studied.

For 152-mm trees only, weight of oven-dry live branchbark was negatively correlated with elevational zone, as follows:

Elevational zone	Weight kg
Low	2.15
Medium	2.08
High	1.78

LATIFOLIA

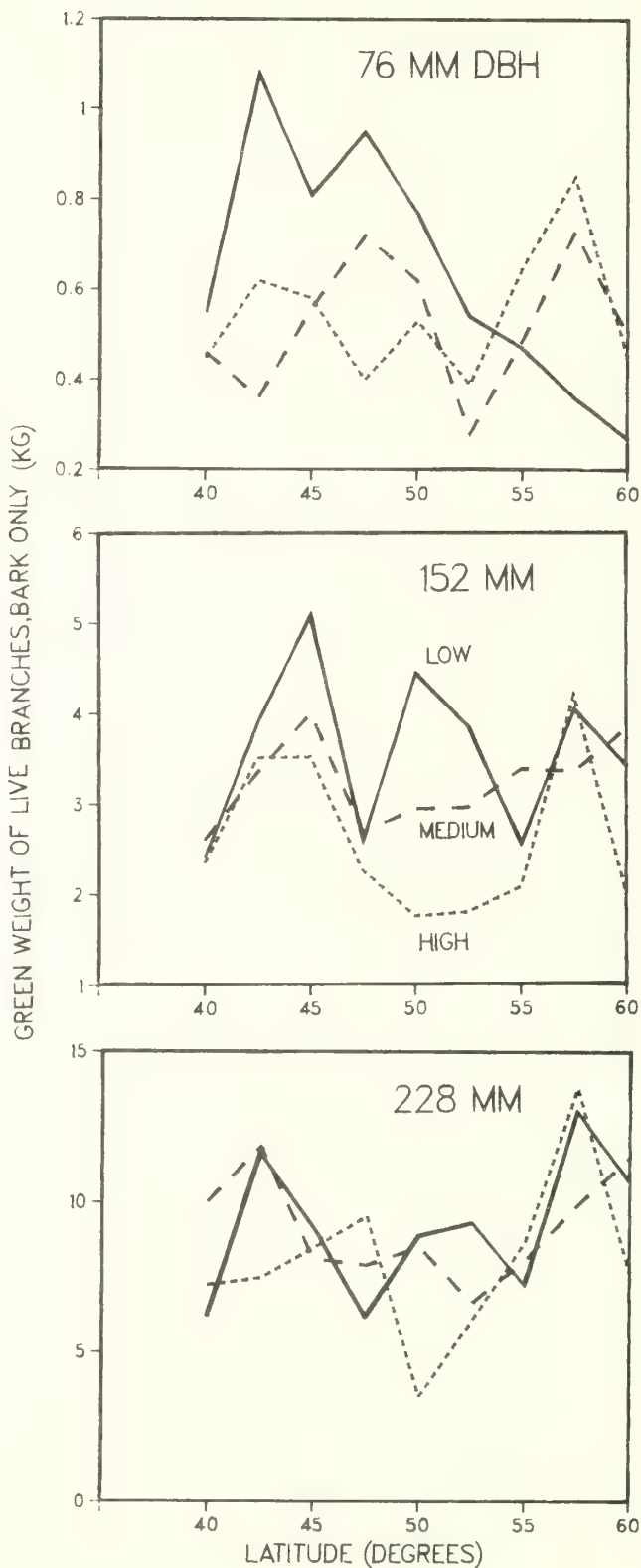


Figure 4-33—Green weight of bark of live branches of *latifolia* trees of three diameters related to latitude and elevational zone.

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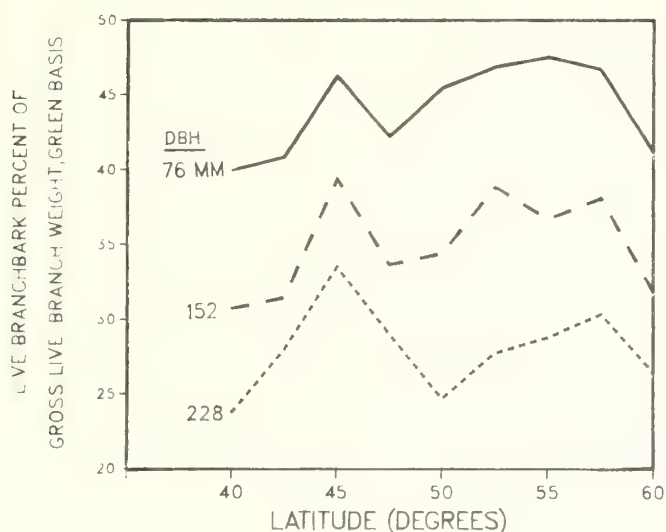


Figure 4-34—Bark as percentage of green weight of foliage-free live branches of *latifolia* trees of three diameters related to latitude.

LATIFOLIA

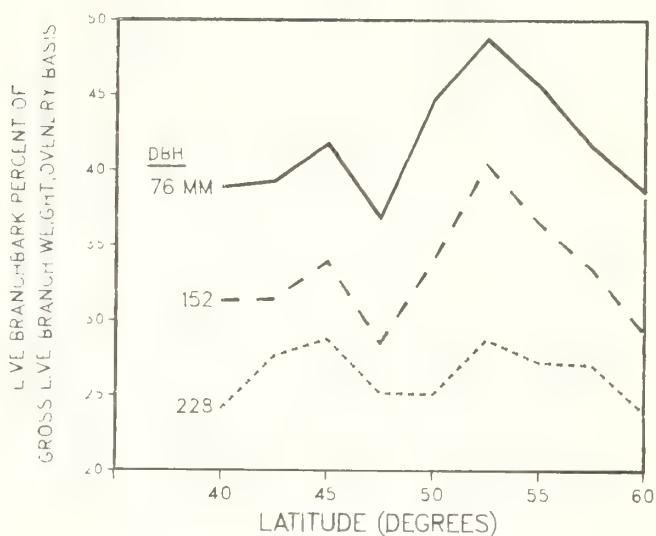


Figure 4-35—Bark as percentage of ovendry weight of foliage-free live branches of *latifolia* trees of three diameters related to latitude

Live Branchbark as Percentage of Gross Live Branch Weight, Green and Ovendry—Bark of live branches averaged 35.72 percent of the weight of green foliage-free branches, with standard deviation of 8.62 percentage points; on an ovendry basis, comparable values were 33.79 and 8.41 percent. Both green and ovendry bark weight percentages were negatively correlated with d.b.h., as follows:

D.b.h.	Green	Ovendry
mm	Percent	Percent
76	44.13 (6.17)	41.78 (6.63)
152	35.01 (5.37)	33.19 (5.50)
228	28.03 (5.08)	26.41 (4.43)

On both green (fig. 4-34) and ovendry (fig. 4-35) bases, branchbark weight percentages were minimum or near minimum (31.49 and 31.43 percent, respectively) at the southernmost latitude of 40 degrees. Maximums averaged 39.71 percent at 45 degrees on a green basis and 39.30 percent at 52.5 degrees on an ovendry basis.

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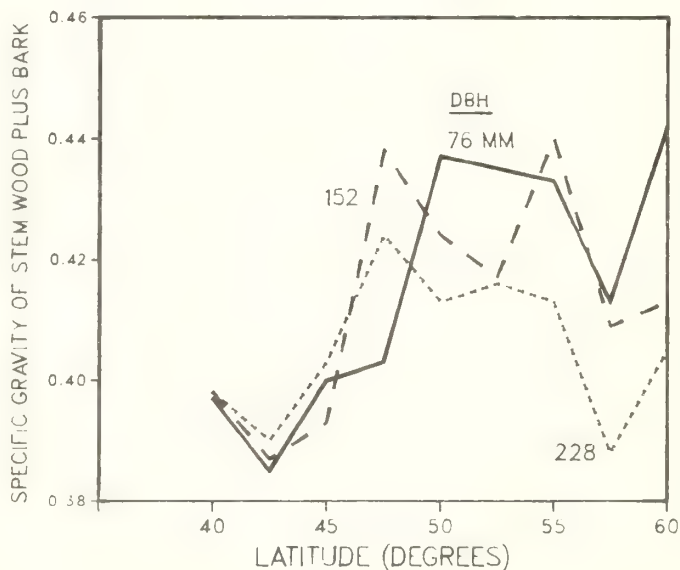


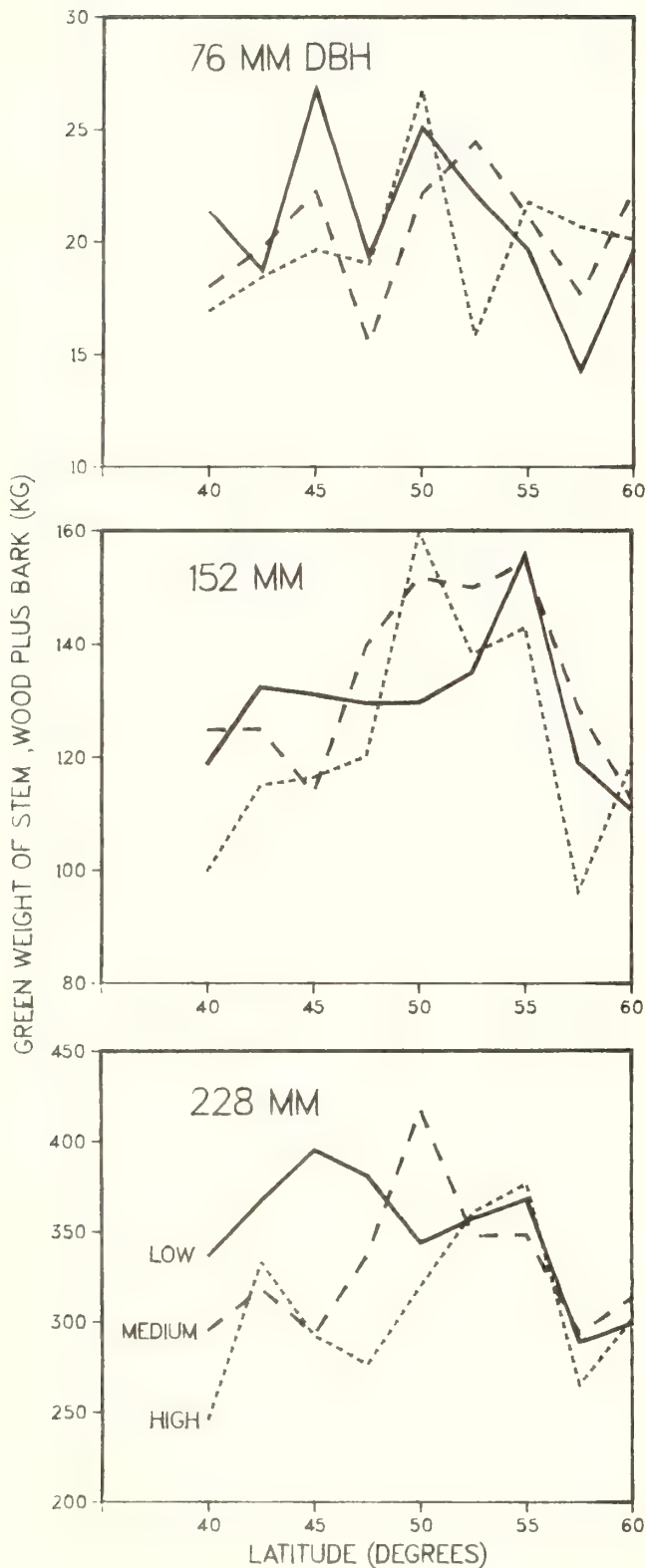
Figure 4-36—Specific gravity (based on ovendry weight and green volume) of stem, wood plus bark, of *latifolia* trees of three diameters related to latitude.

Stem, Wood Plus Bark—Tree Average

Specific Gravity—Wood plus bark of the stems had average specific gravity of 0.412, with standard deviation of 0.030. It was unrelated to elevational zone but was negatively correlated with d.b.h.—particularly in northern latitudes (fig. 4-36), averaging for all latitudes 0.416 (0.036), 0.413 (0.027), and 0.406 (0.025) for trees 76, 152, and 228 mm in d.b.h.

Its relationship with latitude was inverse to that of moisture content (fig. 2-12). Specific gravity was positively correlated with latitude, with minimum average (0.387) at 42.5 degrees and maximum (0.421 or more) from 47.5 degrees north—except at 57.5 degrees where it was 0.403 (fig. 4-36).

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Weight, Green—Trees 76, 152, and 228 mm in d.b.h. had average green stem weights (wood plus bark) of 20.34 (4.37), 128.49 (25.45), and 328.85 (61.81) kg. Green stems from high-elevation zones tended to weigh less than those in low; for example, stems of 228-mm trees from high, medium, and low zones averaged 308.22, 329.59, and 348.73 kg, respectively (fig. 4-37). Because stems (wood plus bark) from northern latitudes have much lower moisture content than those from southern latitudes (fig. 2-12), green stem weight does not vary as much with latitude as oven-dry-weight variation would suggest (figs. 4-37 and 4-38).

Figure 4-37—Green weight of stem, wood plus bark from 152-mm stump height to apical tip, of *latifolia* trees of three diameters related to latitude and elevational zone.

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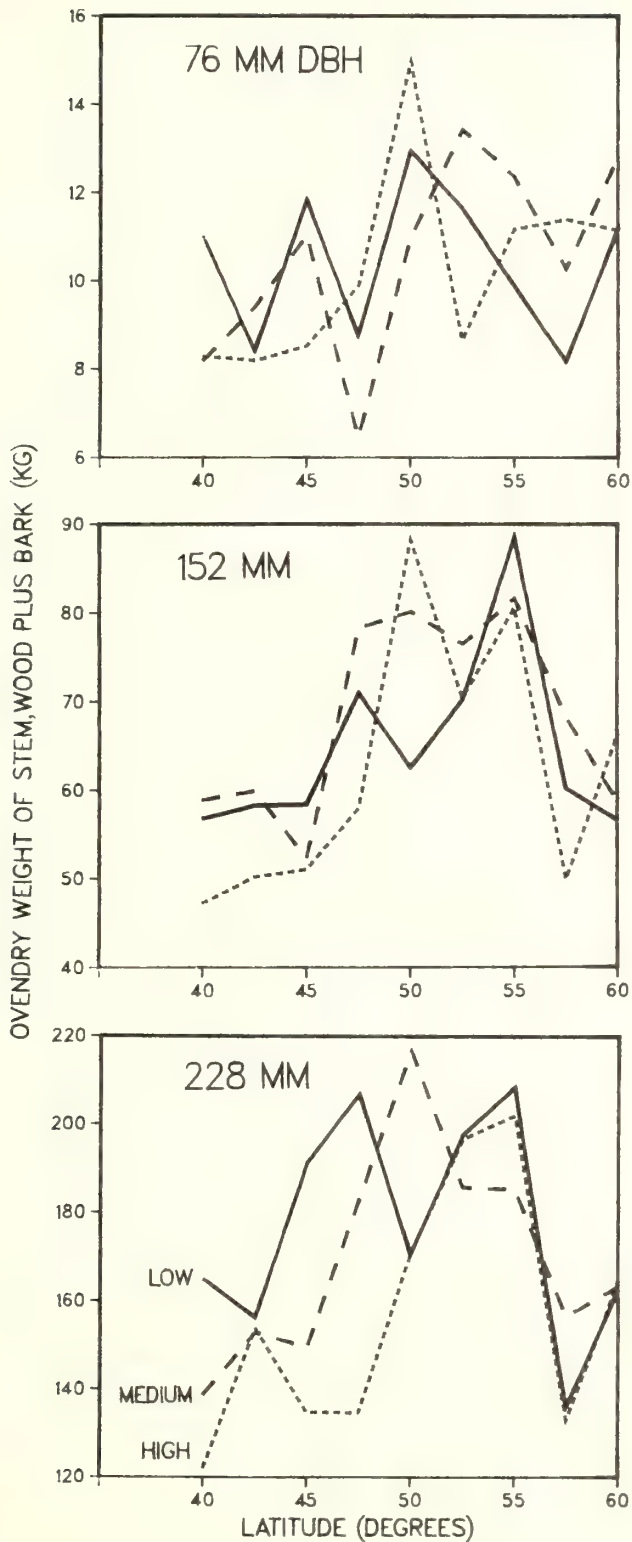


Figure 4-38—Ovendry weight of stem, wood plus bark from 152-mm stump height to apical tip, of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis, stem weight (wood plus bark) increases sharply from southern latitudes to maximums in latitudes from 50 through 55 degrees and then diminishes in the two northernmost latitudes (fig. 4-38). Stems from trees in high-elevation zones weigh less than those from low; with diameter data pooled, ovendry stem weights from low, medium, and high zones averaged 84.11, 83.02, and 76.48 kg (fig. 4-38).

Trees 76, 152, and 228 mm in d.b.h. had average ovendry stem weights (wood plus bark) of 10.35 (2.90), 65.15 (15.49), and 168.12 (34.87) kg.

Green Weight to Yield 1 m³ of Wood—With diameter data pooled, green weight of wood plus bark of stems required to yield 1 m³ of wood averaged 920 kg, with standard deviation of 93 kg. This requirement was unrelated to elevational zone, but was negatively correlated with d.b.h., averaging 968 (105), 920 (74), and 872 (73) kg for trees 76, 152, and 228 mm in d.b.h.

It was negatively correlated with latitude (fig. 4-39), with maximum requirement (981 kg) at 45 degrees and minimum (869 kg) at 57.5 degrees (fig. 4-39).

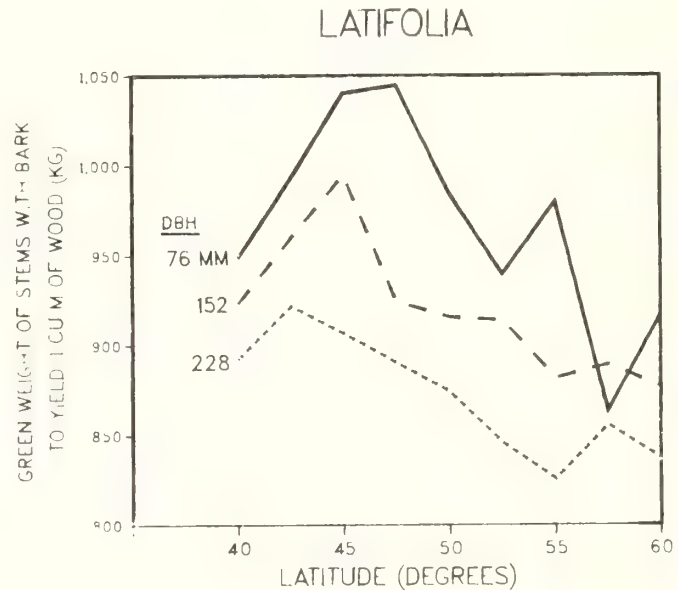


Figure 4-39—Green weight of stems with bark required to yield 1 m³ of bark-free wood from *latifolia* trees of three diameters related to latitude.

Tree Component Proportion, Green-Weight Basis—

Wood plus bark of the stem averaged 73.67 percent of green complete-tree weight including foliage, with standard deviation of 6.64 percentage points. This percentage was unrelated to elevational zone, but was less in 76-mm trees than in larger trees, averaging 71.50 (7.38), 75.09 (5.80), and 74.42 (6.17) for trees 76, 152, and 228 mm in d.b.h.

The percentage was positively correlated with latitude (fig. 4-40); it averaged minimum (71.55 percent) at 42.5 degrees and maximum (75.72 to 76.57 percent) in latitudes 50 through 55 degrees.

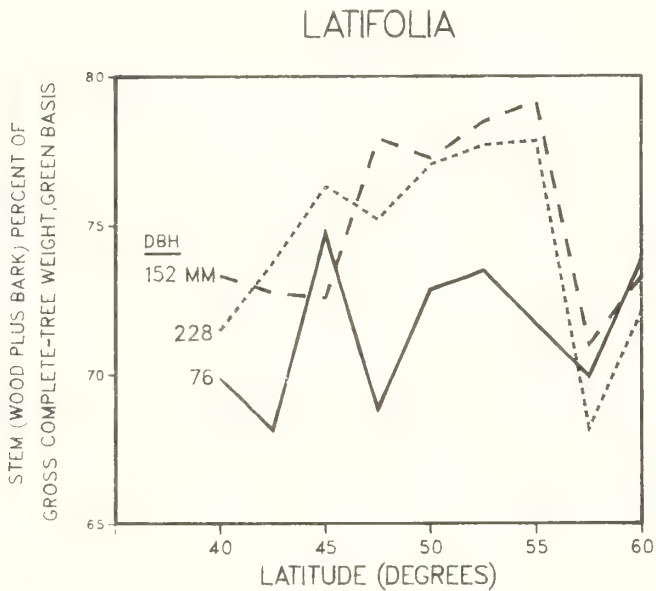


Figure 4-40—Stem (wood plus bark) as percentage of complete-tree green weight, including foliage, of *latifolia* trees of three diameters related to latitude.

Tree Component Proportion, Ovendry-Weight Basis—

On an ovendry-weight basis, wood plus bark of stems averaged 72.79 percent of complete-tree weight including foliage, with standard deviation of 7.13 percentage points. This proportion was unrelated to elevational zone, but was less in 76-mm trees than in larger trees, averaging 71.01 (8.17), 74.00 (6.36), and 73.37 (6.46) percent for trees 76, 152, and 228 mm in d.b.h.

It was positively correlated with latitude (fig. 4-41), with minimum (69.69 percent) at 42.5 degrees and maximums (75.06 to 75.83) in latitudes 50 through 55 degrees.

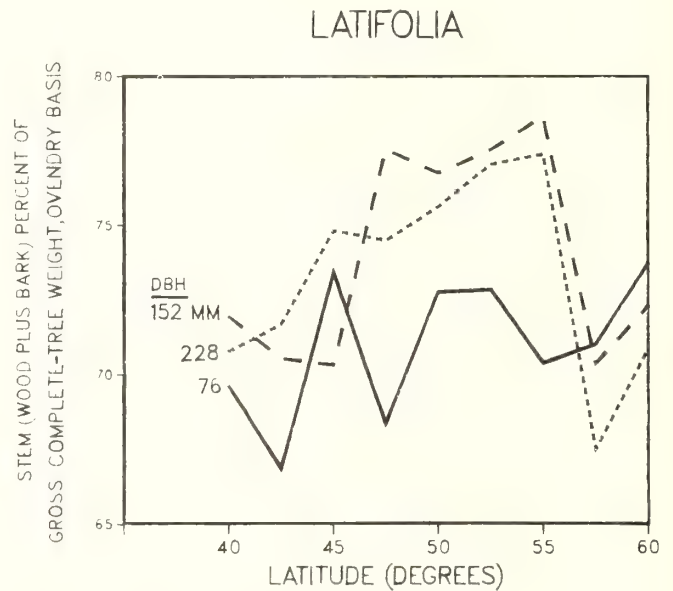


Figure 4-41—Stem (wood plus bark) as percentage of complete-tree ovendry weight, including foliage, of *latifolia* trees of three diameters related to latitude.

Stem, Wood Plus Bark—Variation With Height

Specific Gravity—The specific gravity of stemwood diminishes curvilinearly from stump height up to the base of the live crown and then remains somewhat constant, whereas stembark specific gravity continues to diminish all the way to the apical tip. Stem specific gravity, including both wood and bark, therefore diminishes at an intermediate rate, with a rapid drop near the apical tip where bark proportion is large (fig. 4-42). Levels of the specific gravity patterns differed significantly with diameter. The specific gravity of a disk (wood plus bark) taken at 20 percent of tree height approximates the stem average (fig. 4-42).

Specific gravity-height relationships also varied significantly with latitude (fig. 4-43).

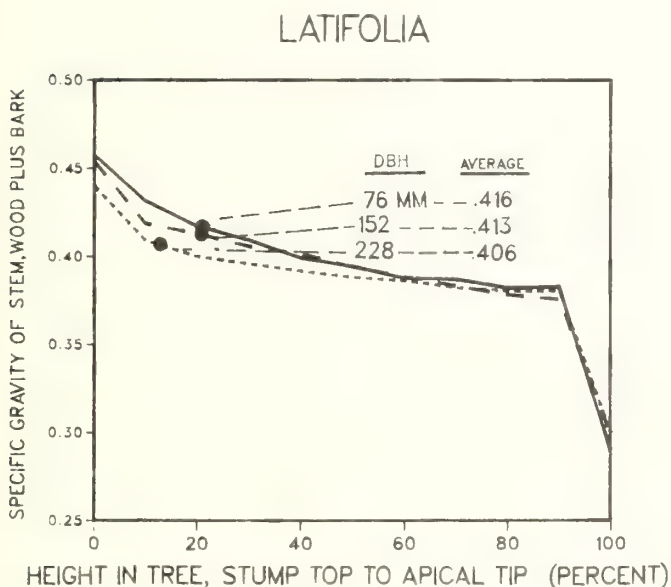


Figure 4-42—Specific gravity of stem (wood plus bark), based on oven-dry weight and green volume, of *latifolia* trees of three diameters related to height in tree.

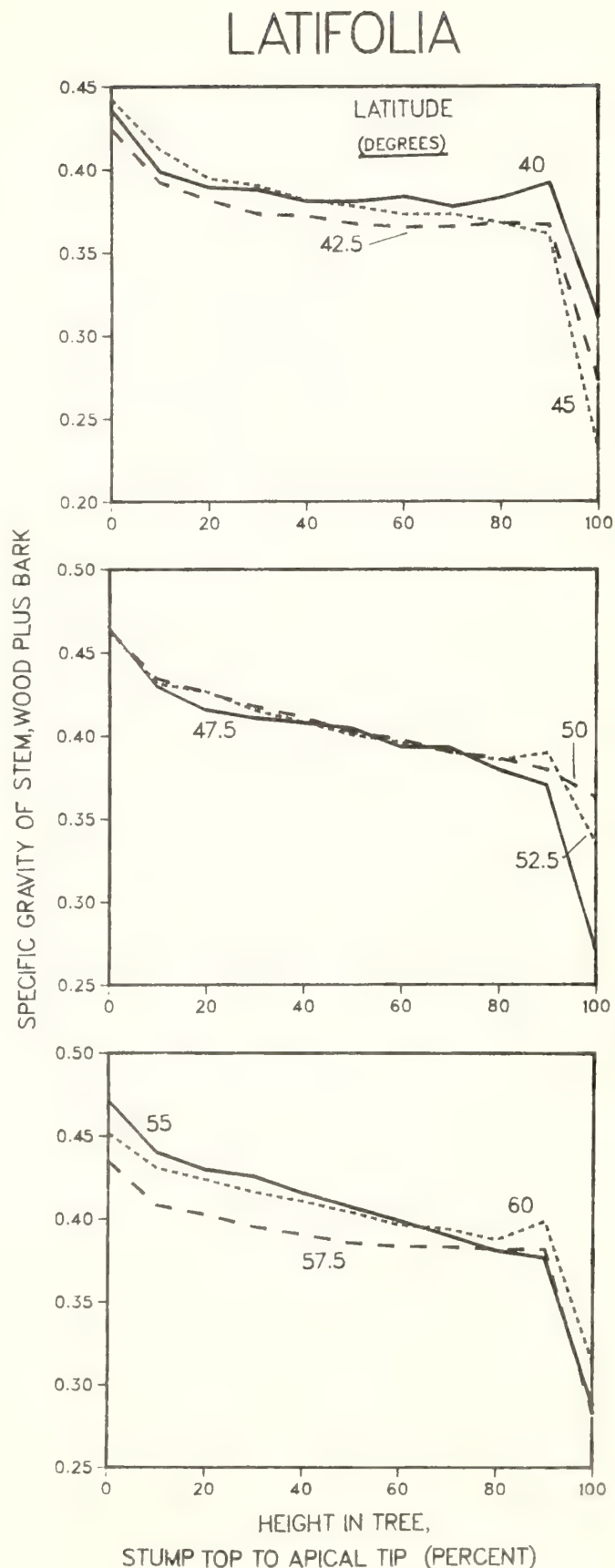


Figure 4-43—Specific gravity of stem (wood plus bark), based on oven-dry weight and green volume, of *latifolia* trees related to height in tree and latitude.

Stemwood—Tree Average

Specific Gravity—With all data pooled, stemwood specific gravity based on ovendry weight and green volume averaged 0.418, with standard deviation of 0.032. It was unrelated to elevational zone, but negatively correlated with d.b.h., averaging 0.427 (0.037), 0.419 (0.028), and 0.407 (0.026) for trees 76, 152, and 228 mm in d.b.h. (fig. 4-44).

The relationship of stemwood specific gravity to latitude (fig. 4-44) was inverse to that of stemwood moisture content (fig. 2-15). That is, stemwood specific gravity was positively correlated with latitude, as follows (diameter and elevational data pooled):

Latitude Degrees	Specific gravity
40	0.401
42.5	.390
45	.408
47.5	.431
50	.430
52.5	.426
55	.435
57.5	.410
60	.427

Average specific gravity (basis of ovendry weight and green volume) of entire stemwood from 152-mm stump height to apical tip in *latifolia* trees of the diameters

studied can be closely estimated from the specific gravity of a complete stemwood disk taken at 20 percent of tree height, by the following relationship ($R^2 = 0.878$; standard error of the estimate = 0.011):

Average stemwood specific gravity =
 $0.07524 + 0.82479$ (stemwood specific gravity
at 20 percent of tree height)

Weight, Green—Because stemwood moisture content is so much less in northern latitudes than in southern (fig. 2-15), green stemwood weight varies less with latitude than ovendry stemwood weights would suggest (figs. 4-45 and 4-46). Green stemwood from trees in low-elevation zones tends to weigh more than that from high zones; with diameter data pooled, green stemwood weights from low, medium, and high zones averaged 322.12, 303.18, and 283.74 kg, respectively (fig. 4-45).

Trees 76, 152, and 228 mm in d.b.h., had average green stemwood weights of 17.63 (3.95), 116.62 (23.83), and 303.01 (58.13) kg, respectively.

Weight, Ovendry—On an ovendry basis, stemwood weights averaged 9.14 (2.56), 59.13 (14.46), and 154.08 (32.58) kg for the three diameter classes. Ovendry stemwood—diameter data pooled—weighed less in trees from high zones (144.01 kg) than that from low zones (162.52 kg), but interactions with diameter and latitude were complex (fig. 4-45). Weight of ovendry stemwood increased sharply from the southernmost latitude to maximums in latitudes from 50 to 55 degrees, and then diminished in the two northernmost latitudes (fig. 4-46).

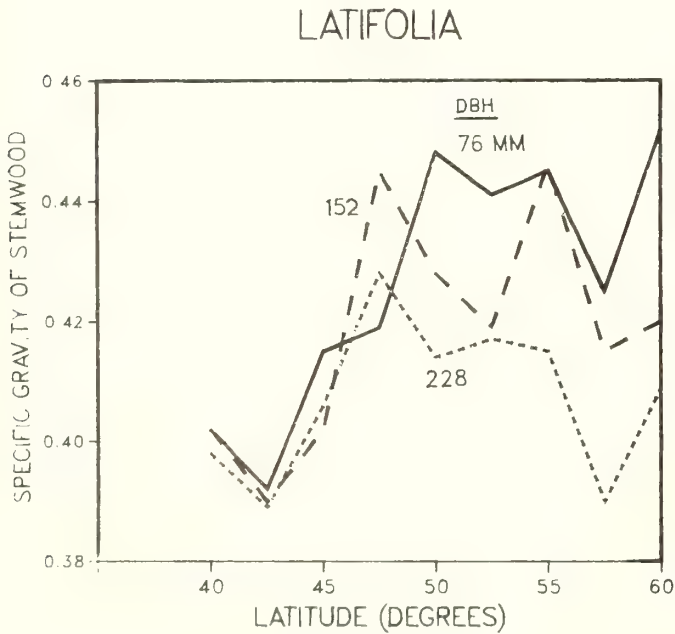


Figure 4-44—Specific gravity of stemwood (152-mm stump height to apical tip), based on ovendry weight and green volume, of *latifolia* trees of three diameters related to latitude.

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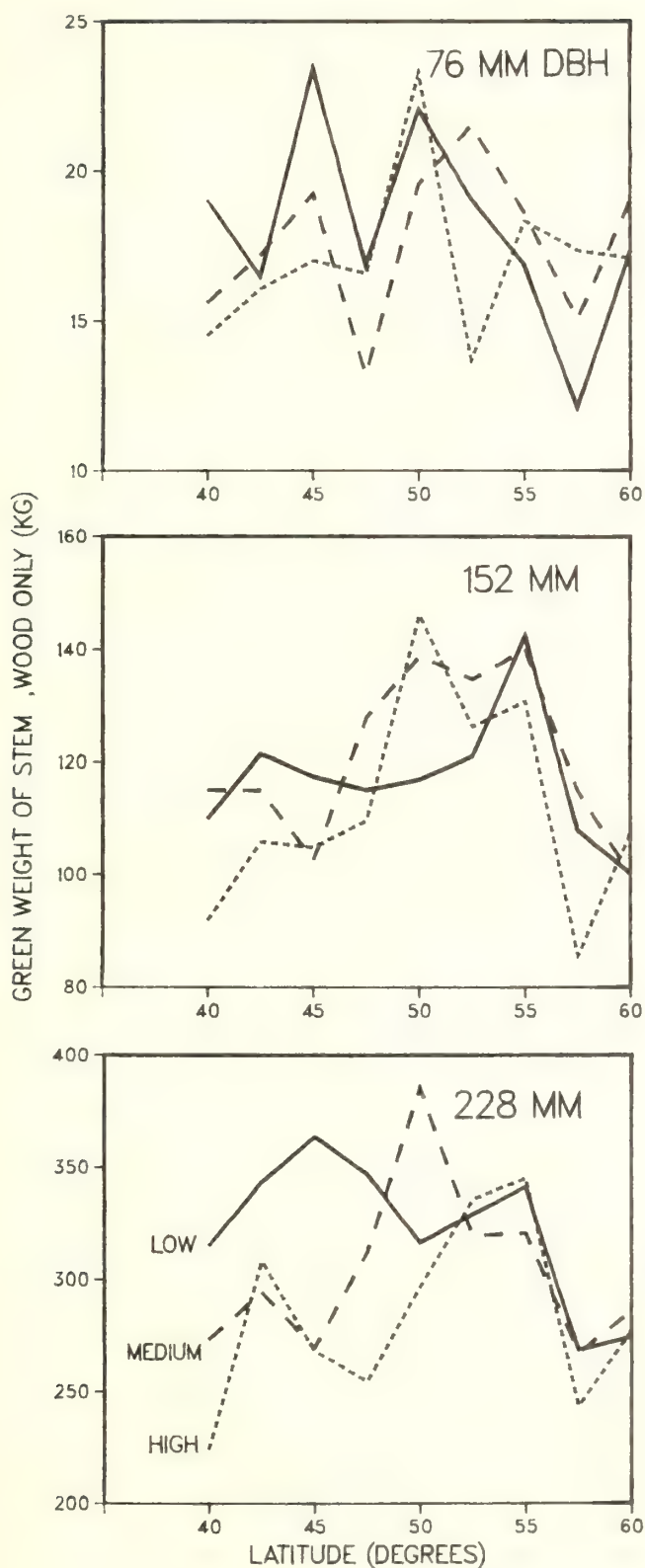


Figure 4-45—Green weight of stemwood from 152-mm stump height to apical tip of *latifolia* trees of three diameters related to latitude and elevational zone.

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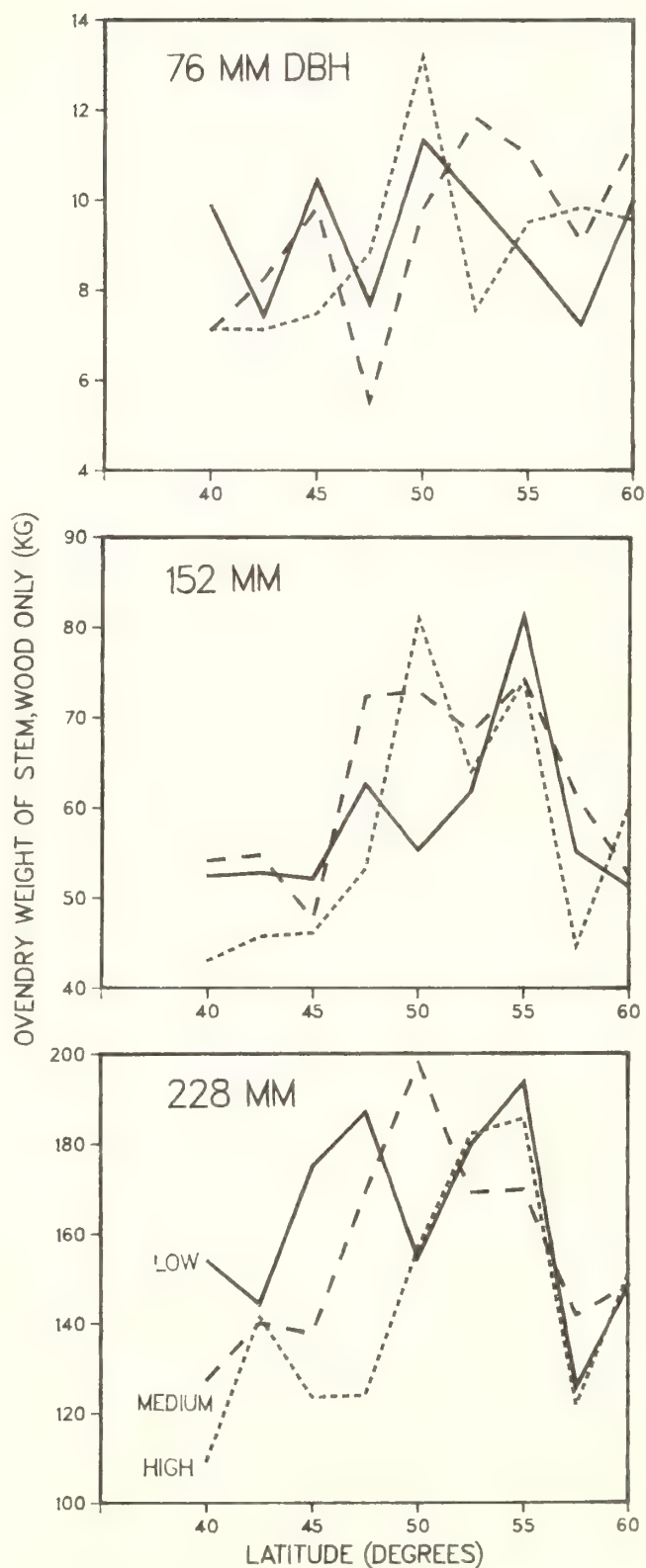


Figure 4-46—Ovendry weight of stemwood from 152-mm stump height to apical tip of *latifolia* trees of three diameters related to latitude and elevational zone.

Stemwood—Variation With Height

Specific Gravity—As previously noted, average stemwood specific gravity can be closely predicted from a stemwood disk taken at 20 percent of tree height. Stemwood specific gravity diminishes curvilinearly from stump top to near the base of the live crown, above which it remains more or less constant—or increases slightly (fig. 4-47, top, and table 4-8). Variation patterns were similar for the three tree diameters studied, but the level of the curves varied significantly with diameter—that is, at all heights small-diameter trees had higher stemwood specific gravity than large trees. At 60 percent of tree height, that is, to just above the base of the live crown, stemwood specific gravity differed little with diameter, however, averaging 0.399, 0.395, and 0.391 for trees 76, 152, and 228 mm in d.b.h. (table 4-9).

Stemwood specific gravity relationship to height in tree also differed significantly with latitude (fig. 4-48).

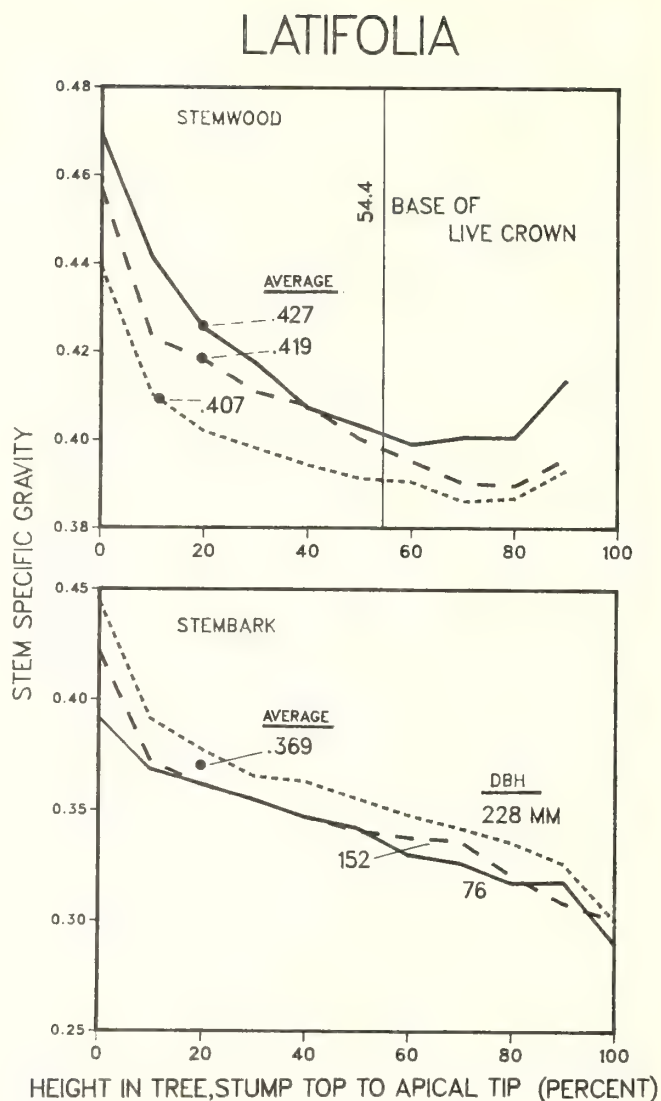


Figure 4-47—Specific gravity of stemwood and stembark (based on oven-dry weight and green volume) of *latifolia* trees of three diameters related to height in tree and base of live crown.

Table 4-8—*Latifolia* stemwood specific gravities (oven-dry weight and green volume) from 152-mm stump height to apical tip at 10 levels in trees of three breast-height diameters¹

Percent of stem height above stump	Diameter		
	76 mm	152 mm	228 mm
0	0.469 (0.044)	0.457 (0.038)	0.439 (0.031)
10	.441 (.041)	.423 (.032)	.410 (.031)
20	.425 (.040)	.418 (.034)	.402 (.030)
30	.417 (.040)	.411 (.033)	.398 (.028)
40	.407 (.041)	.408 (.033)	.394 (.029)
50	.403 (.039)	.400 (.028)	.391 (.032)
60	.399 (.036)	.395 (.025)	.391 (.026)
70	.401 (.040)	.390 (.026)	.386 (.027)
80	.401 (.047)	.390 (.025)	.387 (.026)
90	.414 (.056)	.396 (.034)	.393 (.027)

¹Latitudinal and elevational data pooled; standard deviations shown in parentheses following average values. Data based on 81 trees of each diameter.

Table 4-9—Stemwood specific gravities and stemwood diameters at 60 percent of tree height¹ in *latifolia* trees of three diameters

D.b.h.	Specific gravity ²	Diameter inside bark
mm		mm
76	0.399 (0.036)	47.7 (4.7)
152	.395 (.025)	96.1 (6.6)
228	.391 (.026)	141.4 (10.6)

¹In these *latifolia* trees, the crown base averages about 55 percent of tree height from 152-mm stump height to apical tip.
²Based on oven-dry weight and green volume. The average values are followed by the standard deviation in parentheses.

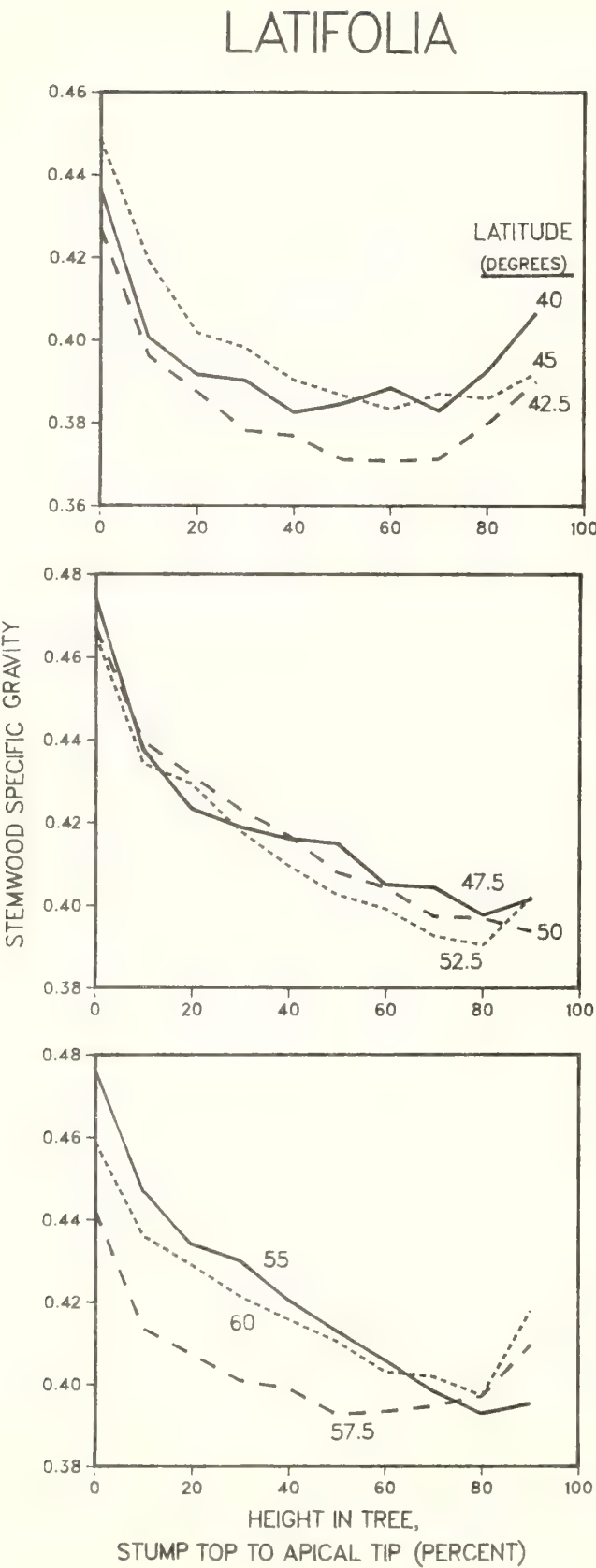


Figure 4-48—Stemwood specific gravity (based on oven-dry weight and green volume) of *latifolia* trees related to height in tree and latitude.

Stembark—Tree Average

Specific Gravity—Stembark specific gravity averaged 0.369, with standard deviation of 0.042, based on oven-dry weight and green volume. It was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 0.356 (0.046), 0.367 (0.038), and 0.383 (0.036) for trees 76, 152, and 228 mm in d.b.h.

Stembark specific gravity varied significantly with latitude (fig. 4-49); it averaged minimum (0.338) at 45 degrees and maximum (0.403) at 52.5 degrees.

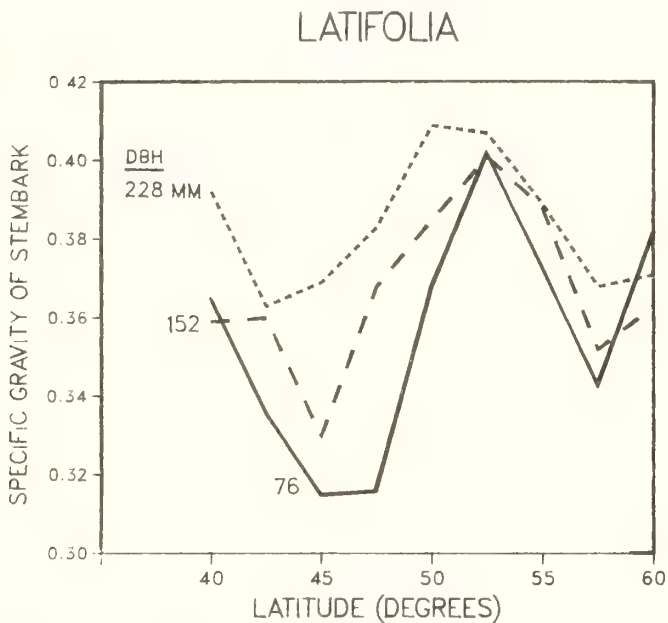


Figure 4-49—Specific gravity of stembark from 152-mm stump height to apical tip (based on oven-dry weight and green volume) of *latifolia* trees of three diameters related to latitude.

Weight, Green—Moisture content of stembark is maximum at about 45 degrees latitude and minimum near 52.5 degrees latitude (fig. 2-18), which yields higher green stembark weights at 45 degrees than oven-dry weights would suggest (figs. 4-50 and 4-51). In high-elevation zones, green stembark from larger trees weighed less than that from low zones (fig. 4-50).

Trees 76, 152, and 228 mm in d.b.h. had green stembark weights averaging 2.71 (0.56), 11.87 (2.62), and 25.83 (5.23) kg, respectively.

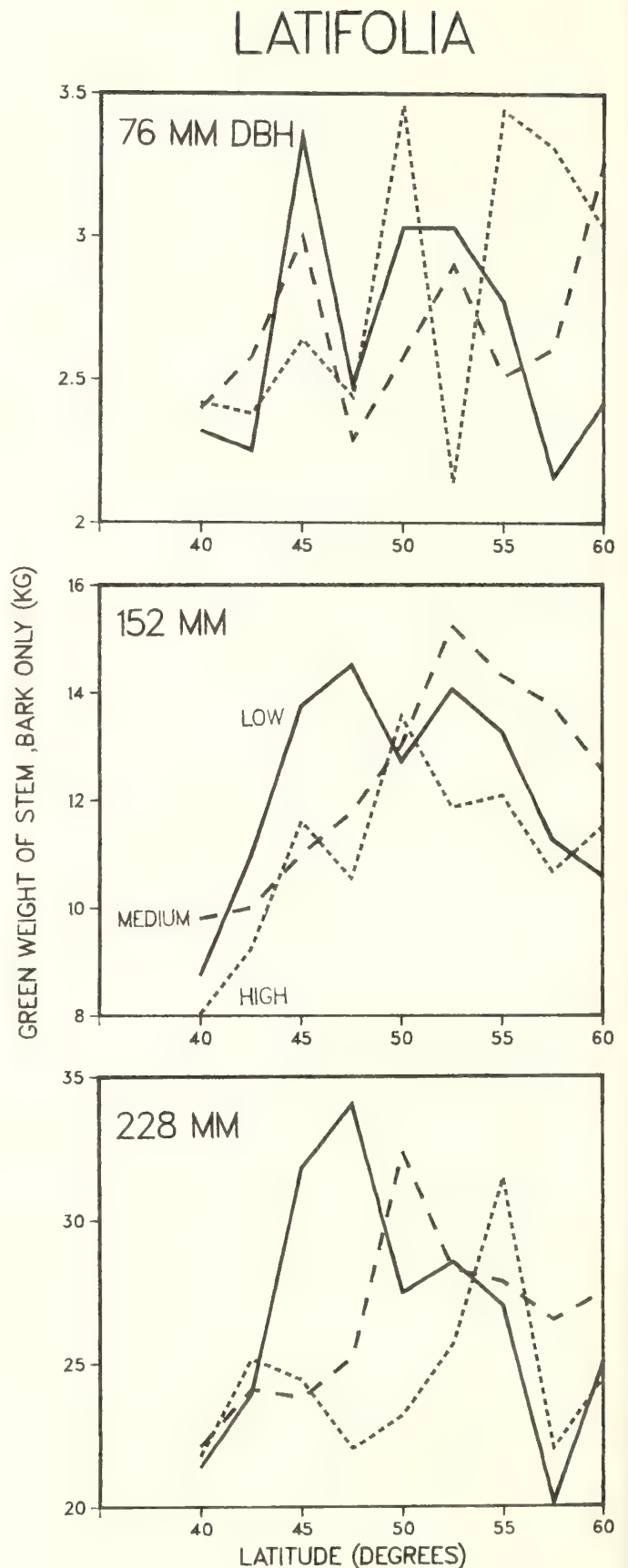


Figure 4-50—Green weight of stembark from 152-mm stump height to apical tip of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis, stembark weight averaged 1.27 (0.32), 6.02 (1.66), and 14.03 (3.37) kg for trees of the three diameter classes. From minimum weights at 40 degrees latitude, ovendry stembark weight increased to maximums in latitudes 47.5 (except for 76-mm trees) through 55 degrees, and then diminished in the two northernmost latitudes (fig. 4-51). In larger trees, stembark from high-elevation zones weighed less than that from low zones (fig. 4-51).

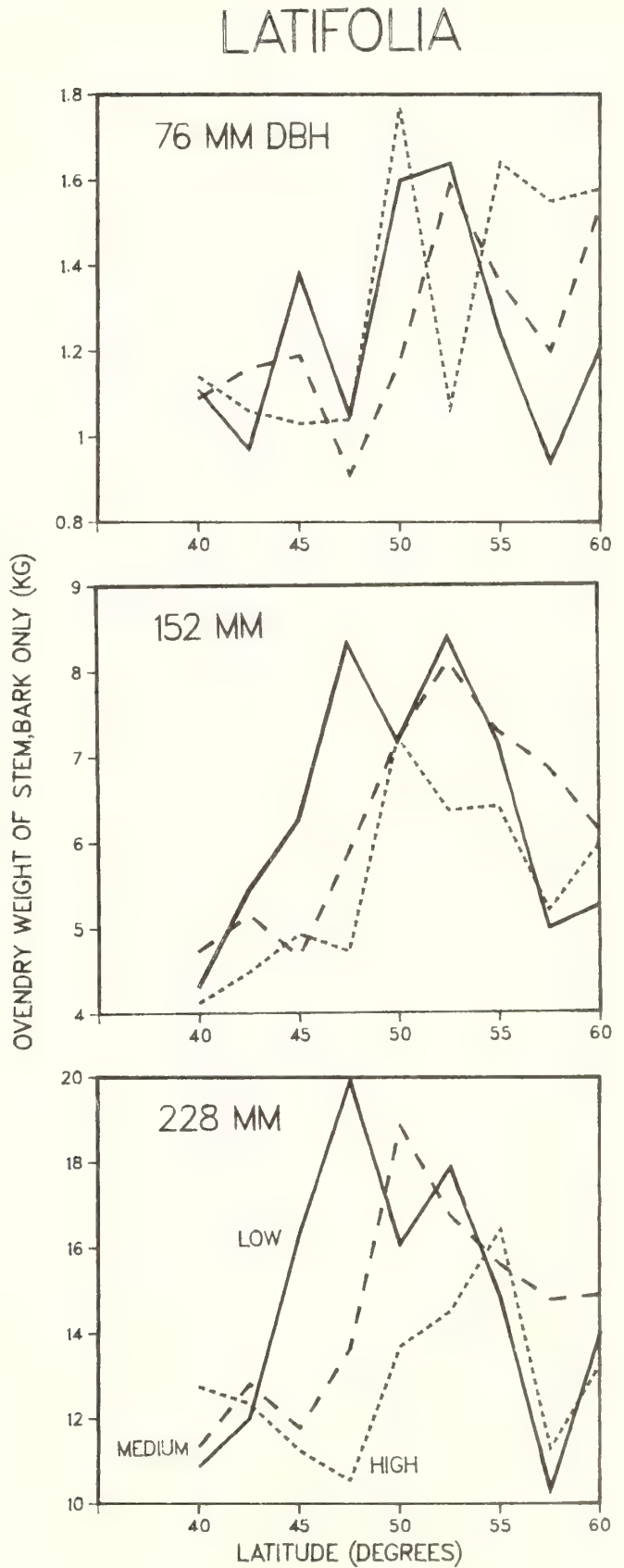


Figure 4-51—Ovendry weight of stembark from 152-mm stump height to apical tip of *latifolia* trees of three diameters related to latitude and elevational zone.

Stembark as Percentage of Gross Stem Weight, Green and Ovendry—On green and ovendry bases, stembark averaged 10.25 and 10.06 percent, with standard deviations of 2.85 and 2.49 percentage points, respectively. Stembark percentage had complex relationships with both elevational zones and latitude (figs. 4-52 and 4-53), and was inversely related to d.b.h as follows:

D.b.h.	Green basis	Ovendry basis
mm	----- Percent -----	
76	13.47 (1.87)	12.38 (1.96)
152	9.35 (1.69)	9.37 (2.03)
228	7.93 (1.19)	8.42 (1.47)

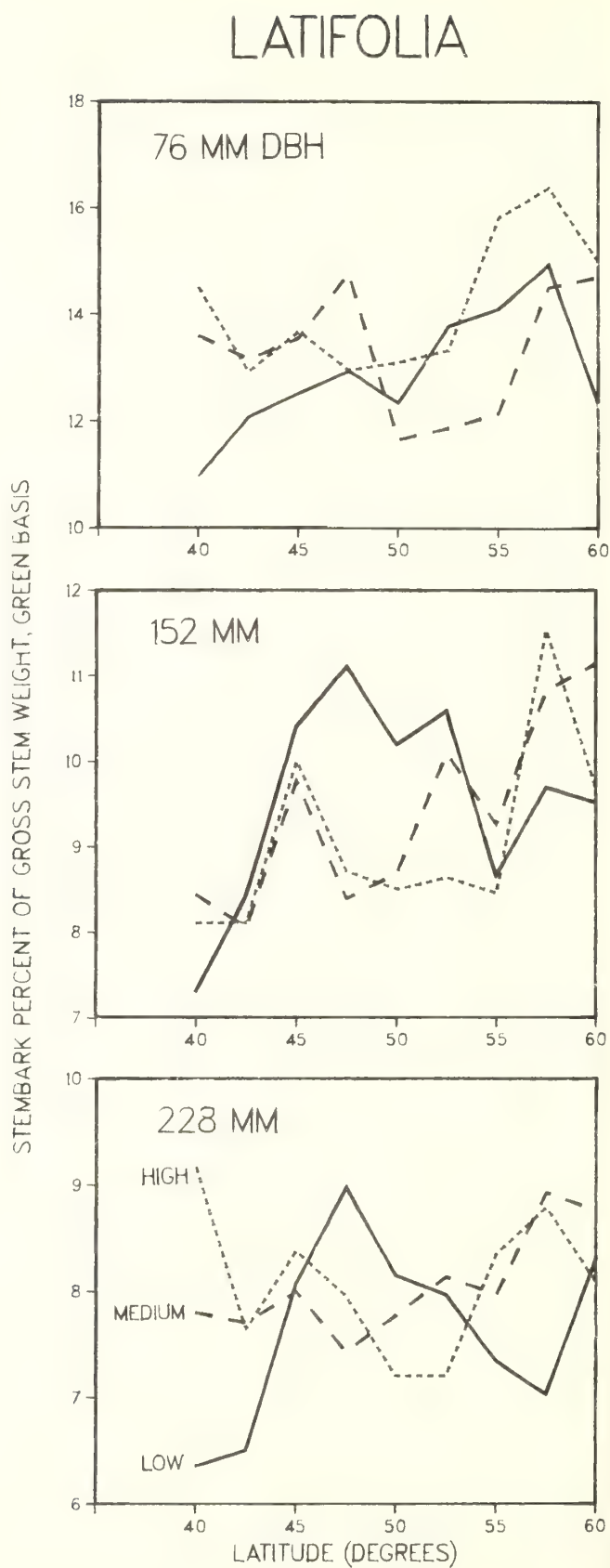


Figure 4-52—Stembark as percentage of gross stem weight (green basis) for *latifolia* trees of three diameters related to latitude and elevational zone.

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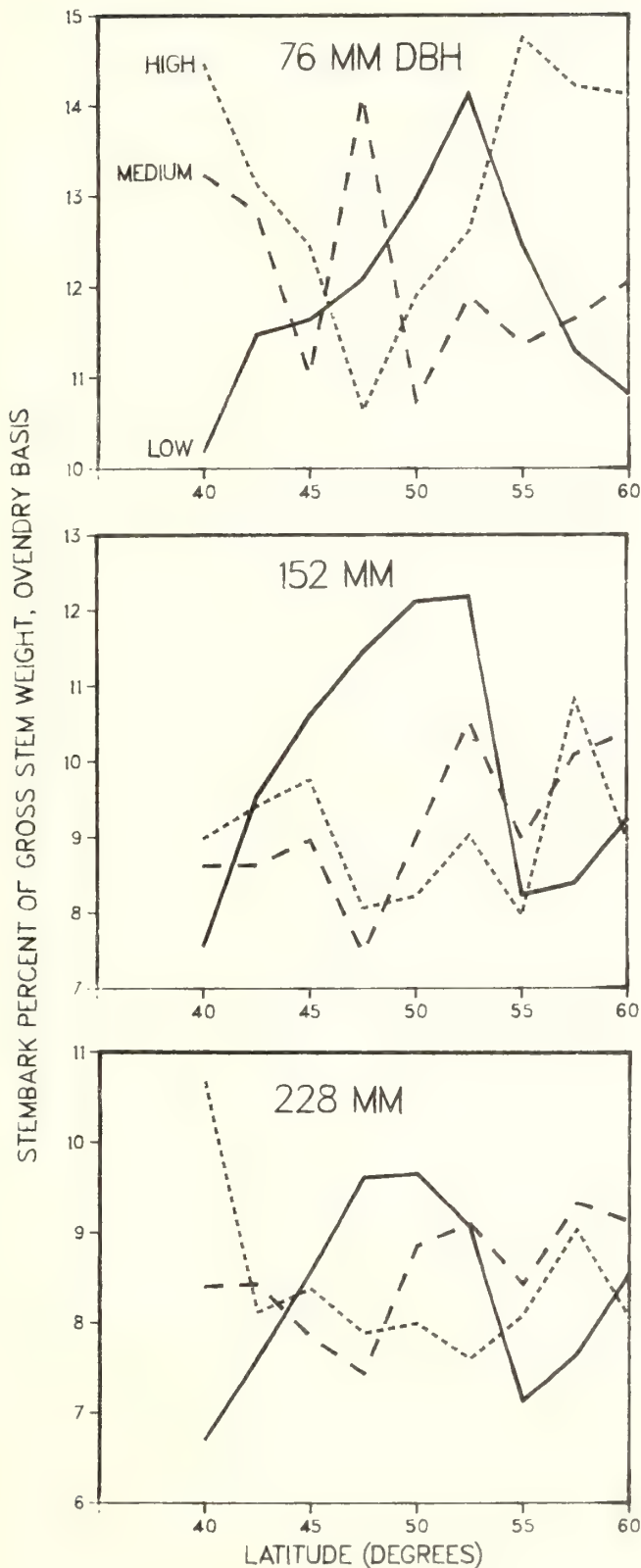


Figure 4-53—Stembark as percentage of gross stem weight (ovendry basis) for *latifolia* trees of three diameters related to latitude and elevational zone.

Stembark—Variation With Height

Specific Gravity—Stembark specific gravity diminishes curvilinearly in an ogee pattern from about 0.42 at stump height to about 0.30 near the apical tip (fig. 4-47, bottom). In contrast to stemwood of trees of the three diameters, stembark specific gravity was greater at all heights in 228-mm trees than in trees of the two smaller diameter classes.

Weight Percentage, Green—Stembark weight as a percentage of green stem sections decreases from stump level to a minimum at about 10 percent of tree height and then increases sharply up the stem to a maximum at the apical tip (fig. 4-54, left). At all heights in the stem, stembark weight percentage is inversely correlated with tree d.b.h.

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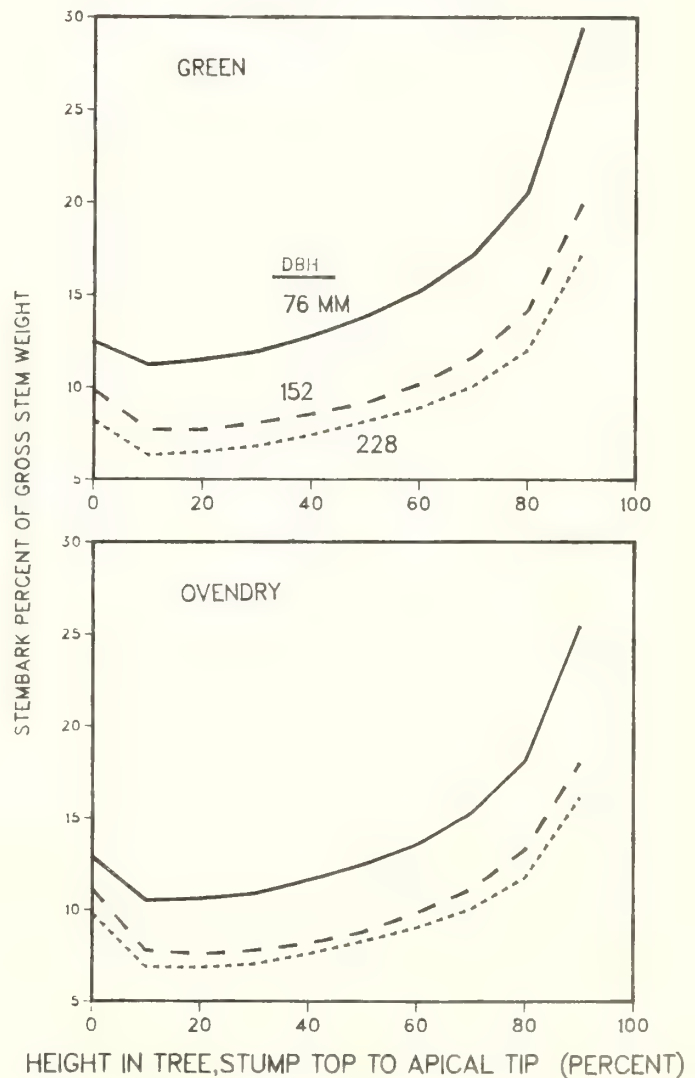


Figure 4-54—Stembark as percentage of gross stem weight, green and ovendry, for *latifolia* trees of three diameters related to height in tree.

On a green-weight basis, stembark from trees in low-elevation zones comprised a lower percentage of stem weight at all heights in the tree (except stump height) than stembark from trees in medium- or high-elevation zones (fig. 4-55).

Also, height variation patterns of stembark weight as percentage of gross green stem weight varied with latitude (fig. 4-56).

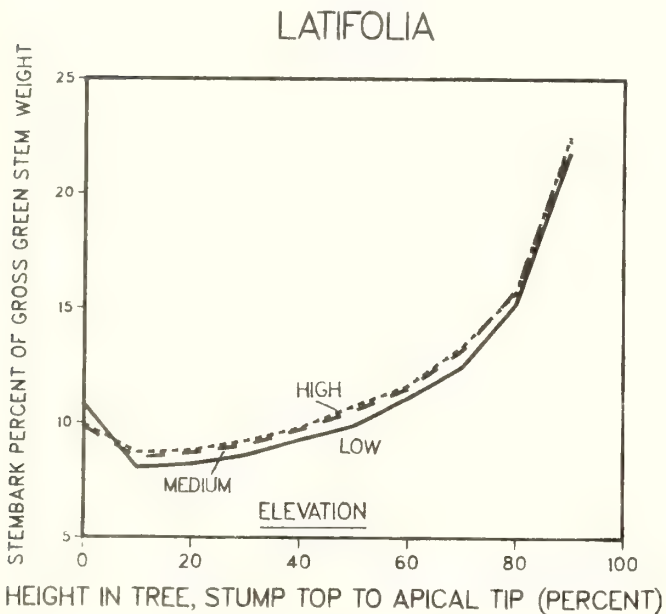


Figure 4-55—Stembark as percentage of gross green stem weight of *latifolia* trees related to height in tree and elevational zone.

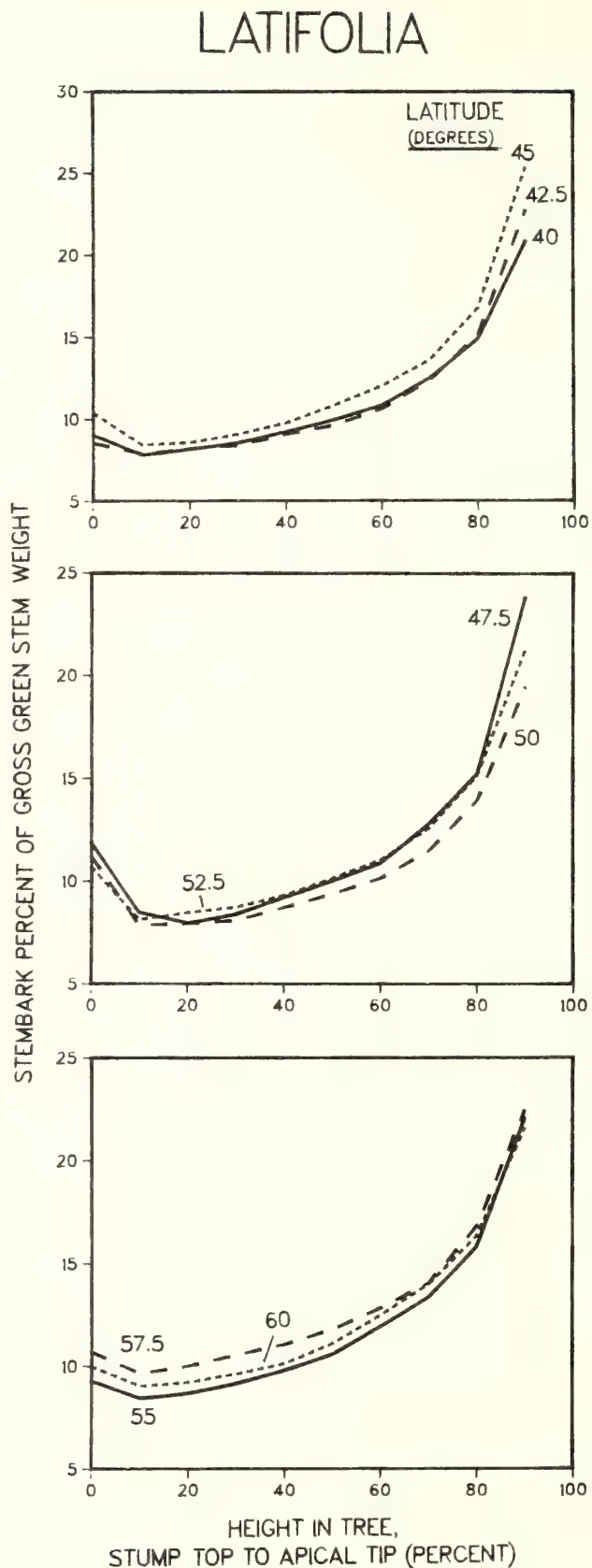


Figure 4-56—Stembark as percentage of gross green stem weight of *latifolia* trees related to height in tree and latitude.

Weight Percentage, Ovendry—On an ovendry-weight basis, stembark weight percentage of stem sections also decreases from stump height to a minimum value at 10 or 20 percent of tree height and then increases curvilinearly up the stem to a maximum at the apical tip (fig. 4-54, right). At all heights, small-diameter trees have a higher weight percentage of stembark than large trees.

Height variation patterns of stembark weight as percentage of gross ovendry stem weight varied with latitude (fig. 4-57).

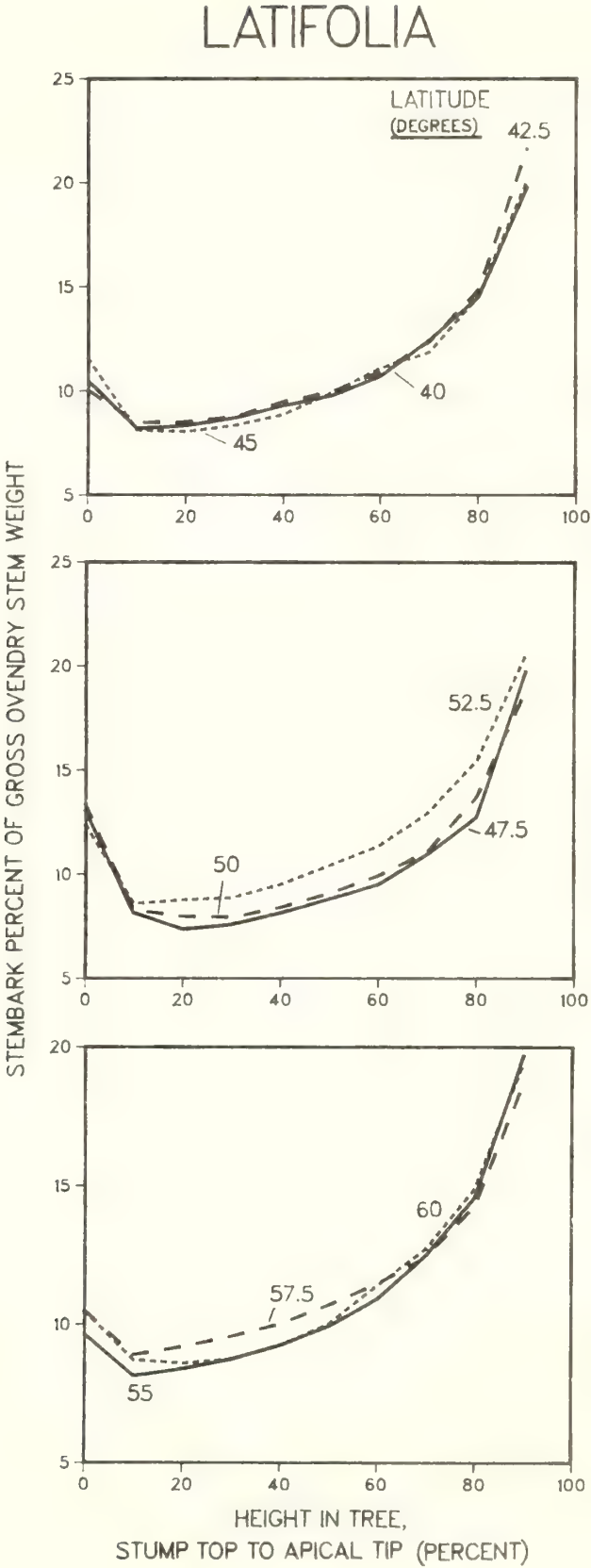


Figure 4-57—Stembark as percentage of gross ovendry stem weight of *latifolia* trees related to height in tree and latitude.

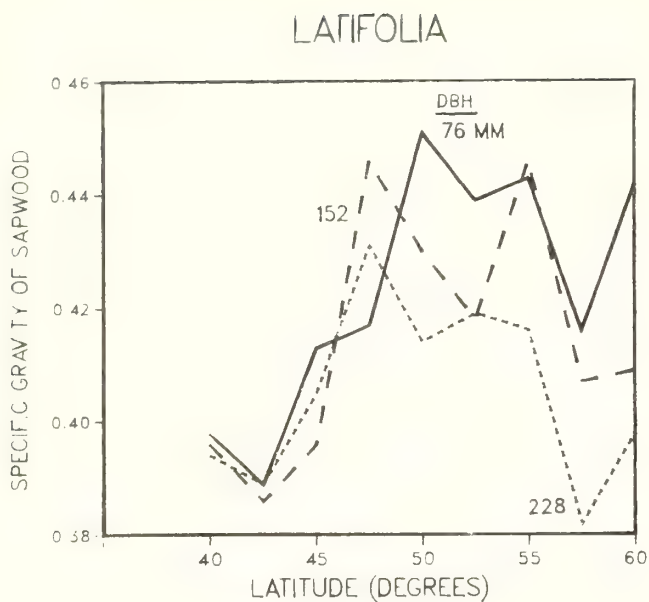


Figure 4-58—Specific gravity of sapwood (based on oven-dry weight and green volume) for *larifolia* trees of three diameters related to latitude.

Sapwood

For additional information on sapwood characteristics see chapter 5.

Specific Gravity—Sapwood specific gravity in the entire stem (oven-dry weight and green-volume basis) was less than that of heartwood, averaging 0.414, with standard deviation of 0.034. Like whole stemwood specific gravity, it was negatively correlated with d.b.h., averaging 0.423 (0.039), 0.415 (0.032), and 0.405 (0.030) for trees 76, 152, and 228 mm in d.b.h.; diameter-related differences were more pronounced in northern than in southern latitudes (fig. 4-58).

Sapwood specific gravity averaged maximum (0.425 to 0.435) at middle latitudes of 47.5 through 55 degrees and minimum (0.396) at 40 degrees (fig. 4-58).

Weight, Green—Sapwood green weight was positively correlated with d.b.h. (fig. 4-59), averaging 14.37 (4.27), 91.34 (23.70), and 226.16 (60.87) kg for trees of the three diameter classes. It was negatively correlated with elevational zone, particularly in 228-mm trees, as follows:

Elevational zone	76 mm d.b.h.	152 mm d.b.h.	228 mm d.b.h.
----- Kilograms -----			
Low	15.19	94.82	248.38
Medium	14.39	94.61	221.86
High	13.53	84.60	208.23

Sapwood green weight was also negatively correlated with latitude, diminishing slightly in northern latitudes (fig. 4-59).

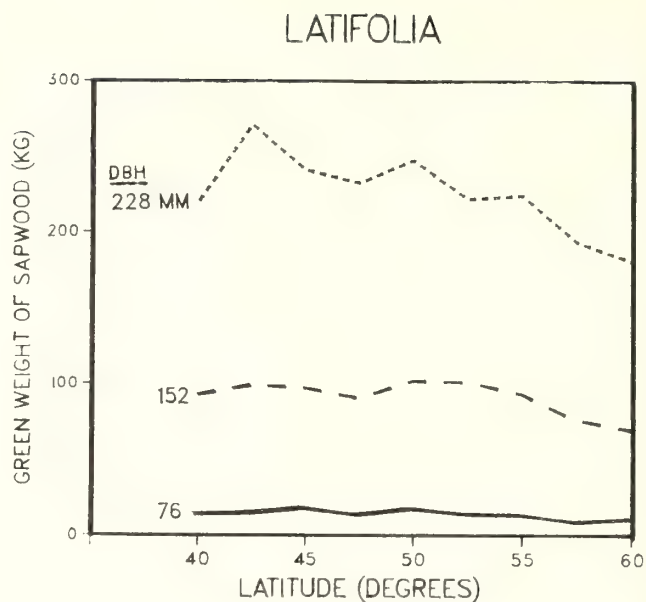


Figure 4-59—Green weight of sapwood in stems from 152-mm stump height to apical tip in *larifolia* trees of three diameters related to latitude.

Weight, Oven-dry—Oven-dry sapwood weight was also positively correlated with d.b.h., averaging 6.89 (2.00), 41.45 (10.78), and 99.81 (24.88) kg for trees 76, 152, and 228 mm in d.b.h. In 228-mm trees, oven-dry sapwood weight was negatively correlated with elevational zone, averaging 109.91, 98.13, and 91.40 kg in low, medium, and high zones, respectively.

As with green sapwood weight, oven-dry weight had a slight negative correlation with latitude (fig. 4-60).

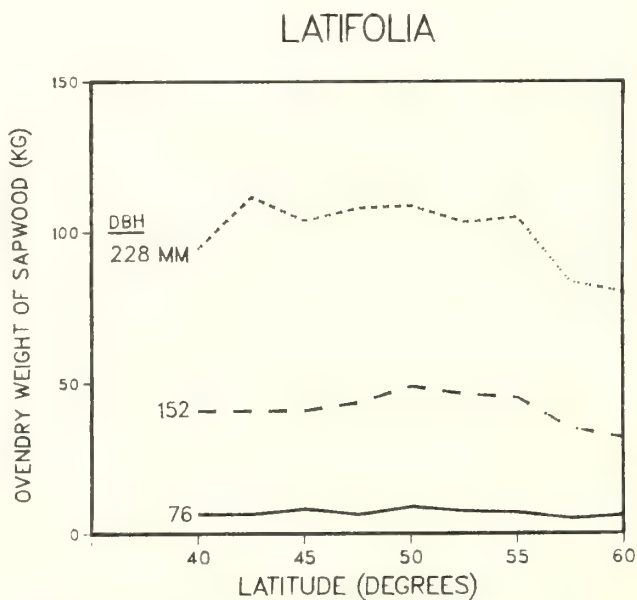


Figure 4-60—Oven-dry weight of sapwood in stems from 152-mm stump height to apical tip in *larifolia* trees of three diameters related to latitude.

Heartwood

For heartwood information additional to that in the following paragraphs, see chapter 5.

Specific Gravity—Heartwood specific gravity in the entire stem averaged 0.434, with standard deviation of 0.034, based on ovendry weight and green volume. It was unrelated to elevational zone and latitude, but was negatively correlated with d.b.h., averaging 0.459 (0.038), 0.430 (0.022), and 0.412 (0.022) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—Weight of green heartwood was positively correlated with d.b.h. (fig. 4-61), averaging 3.26 (2.51), 25.28 (16.15), and 76.85 (37.92) kg for trees 76, 152, and 228 mm in d.b.h. It was generally also positively correlated with elevational zone, averaging as follows for trees of the three diameters:

Elevational zone	76 mm	152 mm	228 mm
----- Kilograms -----			
Low	2.94	22.02	73.74
Medium	3.28	26.34	81.32
High	3.56	27.46	75.50

Green heartwood weight was also positively correlated with latitude, with the relationship most pronounced in large trees (fig. 4-61).

Weight, Ovendry—As with green weight, ovendry heartwood weight was positively correlated with d.b.h. (fig. 4-62), averaging 2.25 (1.78), 17.86 (11.34), and 54.27 (26.23) kg for trees of the three diameter classes. It was also generally positively correlated with elevational zone, averaging as follows for trees of the three diameters:

Elevational zone	76 mm	152 mm	228 mm
----- Kilograms -----			
Low	2.02	15.83	52.61
Medium	2.29	18.65	57.59
High	2.46	19.09	52.61

As with green heartwood, weight of ovendry heartwood was positively correlated with latitude; the relationship was most pronounced in trees of large diameter (fig. 4-62).

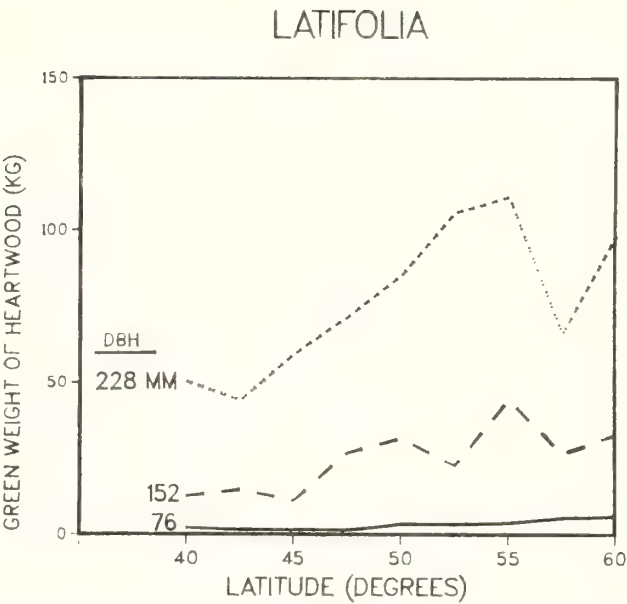


Figure 4-61—Green weight of heartwood in stems from 152-mm stump height to apical tip in *latifolia* trees of three diameters related to latitude.

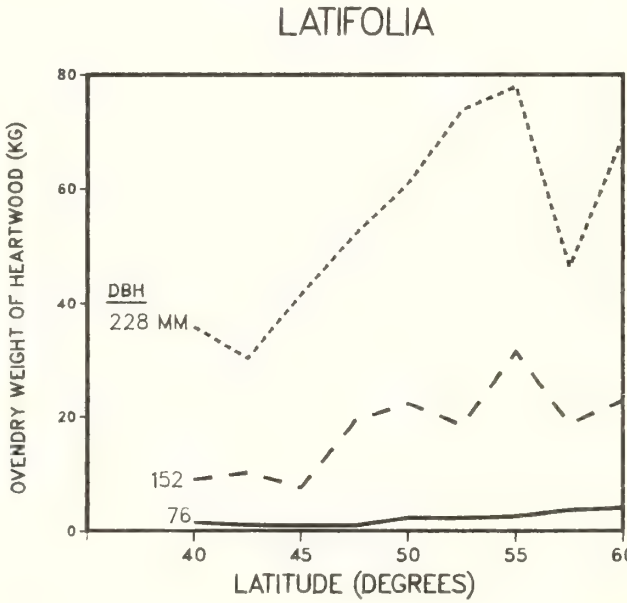


Figure 4-62—Ovendry weight of heartwood in stems from 152-mm stump height to apical tip in *latifolia* trees of three diameters related to latitude.

Ovendry Weight as Percentage of Stemwood—

Heartwood ovendry weight as percentage of stemwood was positively correlated with d.b.h. (fig. 4-63), averaging 22.63 (16.29), 28.78 (15.31), and 34.58 (13.39) percent for trees 76, 152, and 228 mm in d.b.h. It was also positively correlated with latitude, averaging (with diameter data pooled) minimum (18.01 percent) at 42.5 degrees and maximum (43.00 percent) at 60 degrees (fig. 4-63). For all trees studied, it averaged 28.67 percent, with standard deviation of 15.76 percent.

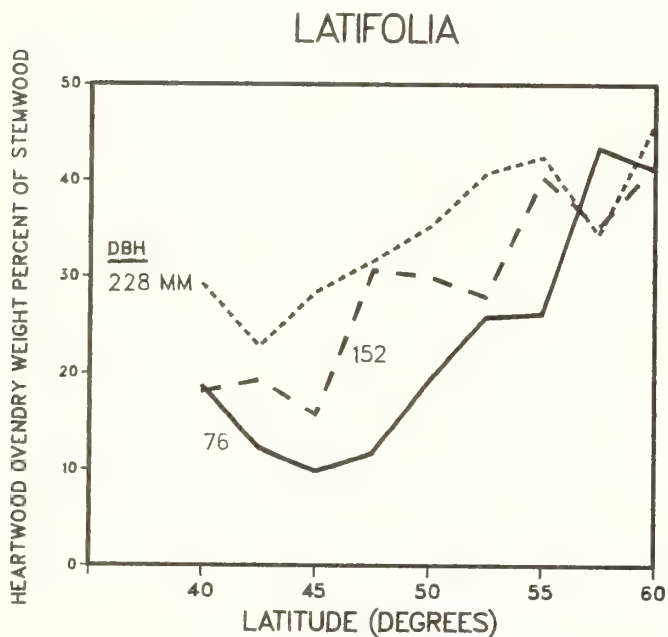


Figure 4-63—Heartwood ovendry weight as percentage of stemwood in *latifolia* trees of three diameters related to latitude.

Stump-Root System, Wood Plus Bark

Specific Gravity—Specific gravity—based on ovendry weight and green volume—of the stump-root system (wood plus bark) is higher than that of stem or branches (table 4-2), averaging 0.461, with standard deviation of 0.043. It increases from a minimum (0.43) at 42.5 degrees to maximums (0.47 to 0.49) from 47.5 through 55 degrees, but is poorly correlated with elevational zone or tree d.b.h. (fig. 4-64).

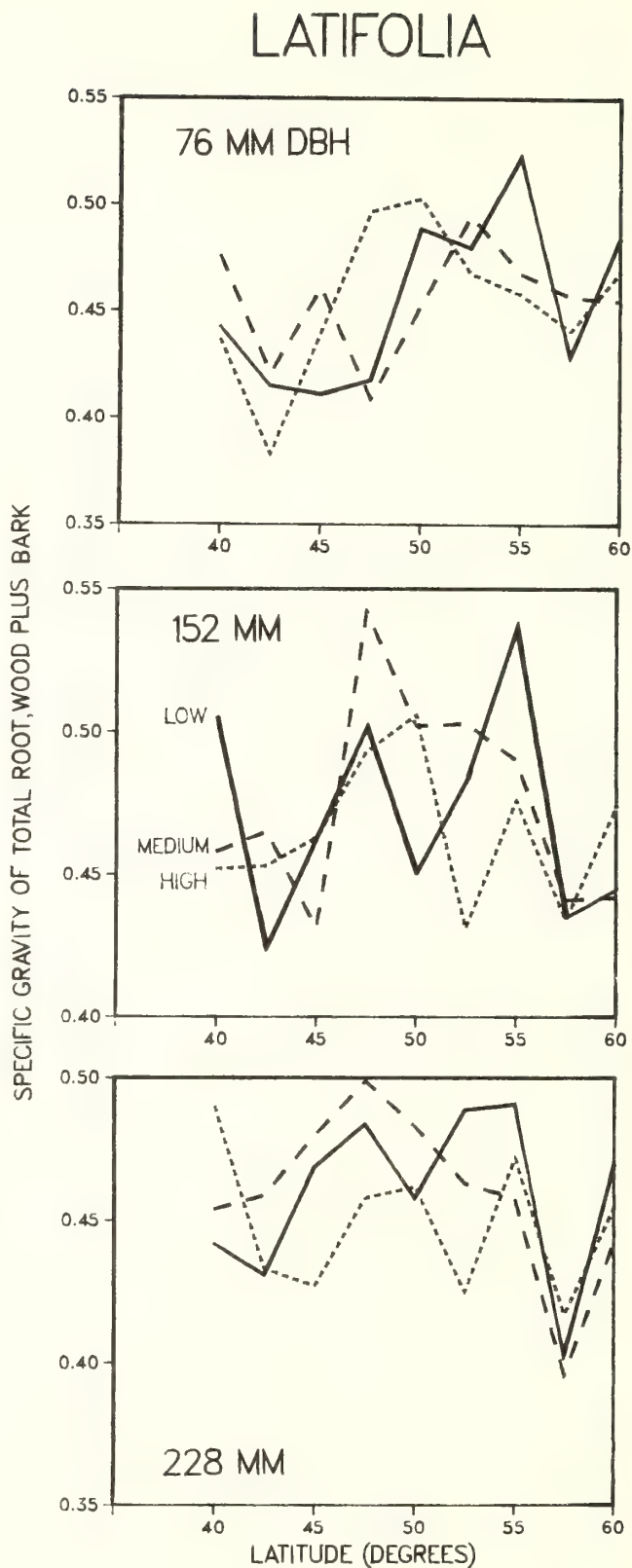


Figure 4-64—Specific gravity of the stump-root system (wood plus bark of stump to 152-mm height, central root mass-taproot, and lateral roots to a radius of 305 mm from stump pith) based on ovendry weight and green volume of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Green—Green weight of the stump-root system, wood plus bark, including 152-mm-high stump, lateral roots to a 305-mm radius from stump pith, and the recovered portion of the taproot was positively correlated with d.b.h., averaging 3.82 (0.89), 18.86 (3.14), and 43.22 (6.84) kg for trees 76, 152, and 228 mm in d.b.h. There was no pronounced latitudinal trend in this green weight, but stump-root systems from high-elevation zones tended to weigh less than those from low zones (fig. 4-65), averaging 22.87, 22.07, and 20.95 kg for low, medium, and high zones (diameter data pooled).

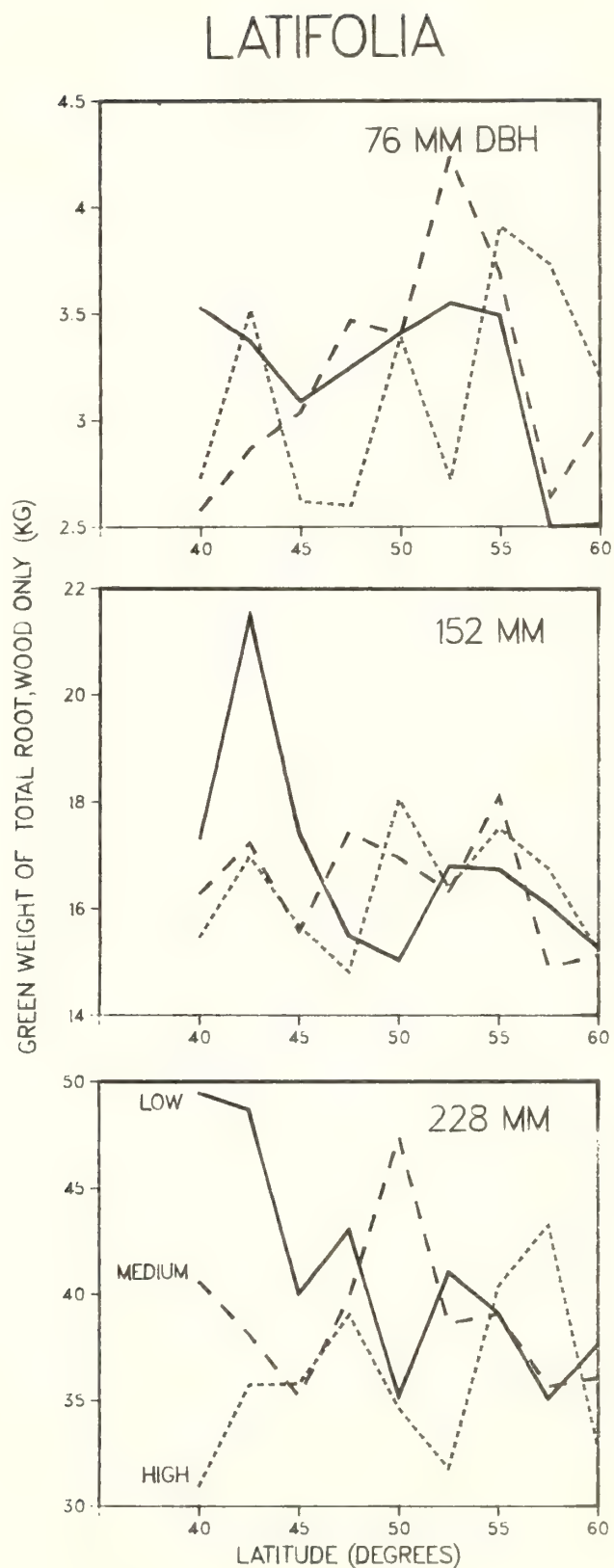


Figure 4-65—Green weight of stump-root systems, wood plus bark, of *latifolia* trees of three diameters related to latitude and elevational zone.

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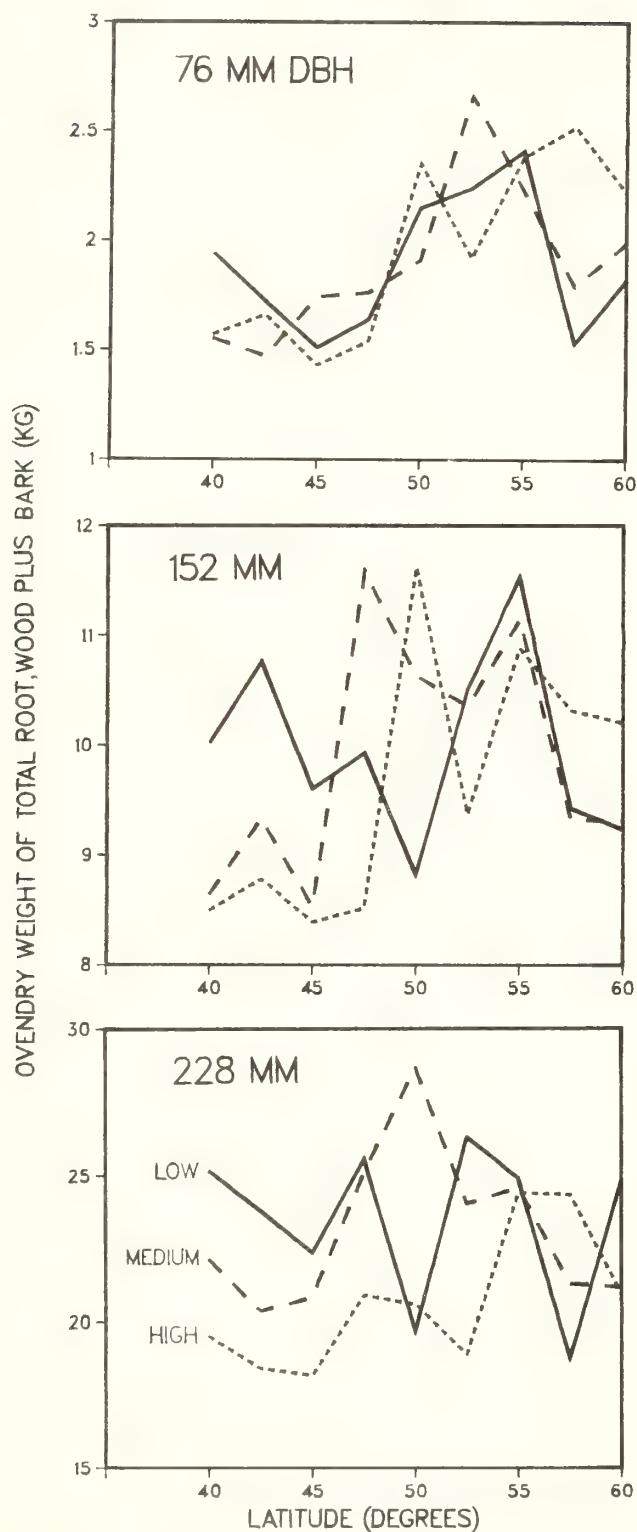


Figure 4-66—Ovendry weight of stump-root systems, wood plus bark, of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—Similarly, strong latitudinal trends were not evident in ovendry weights of the stump-root system, wood plus bark (fig. 4-66). In the larger trees there was a tendency for those from high-elevation zones to have about 10 percent less stump-root weight than those from low zones. Ovendry stump-root weights were positively correlated with d.b.h., averaging 1.91 (0.46), 9.82 (1.17), and 22.43 (3.43) kg for trees of the three diameter classes.

Green Weight to Yield 1 m³ of Wood—Less green weight of stump-root system is required to yield a cubic meter of bark-free wood than weight of live branches (table 4-6); for stump roots it averages 1,046 kg, with standard deviation of 99 kg. This weight requirement is negatively correlated with d.b.h., averaging 1,109 (89), 1,044 (82), and 984 (82) kg for trees 76, 152, and 228 mm in d.b.h.

The weight requirement to yield a cubic meter of bark-free wood diminishes from south to north, averaging 1,093 kg in the four southern latitudinal zones, but only 1,007 kg in the five northern zones (fig. 4-67). In low-elevation zones slightly more weight (1,054 kg) is required, on average, than from medium and high zones (1,041 kg).

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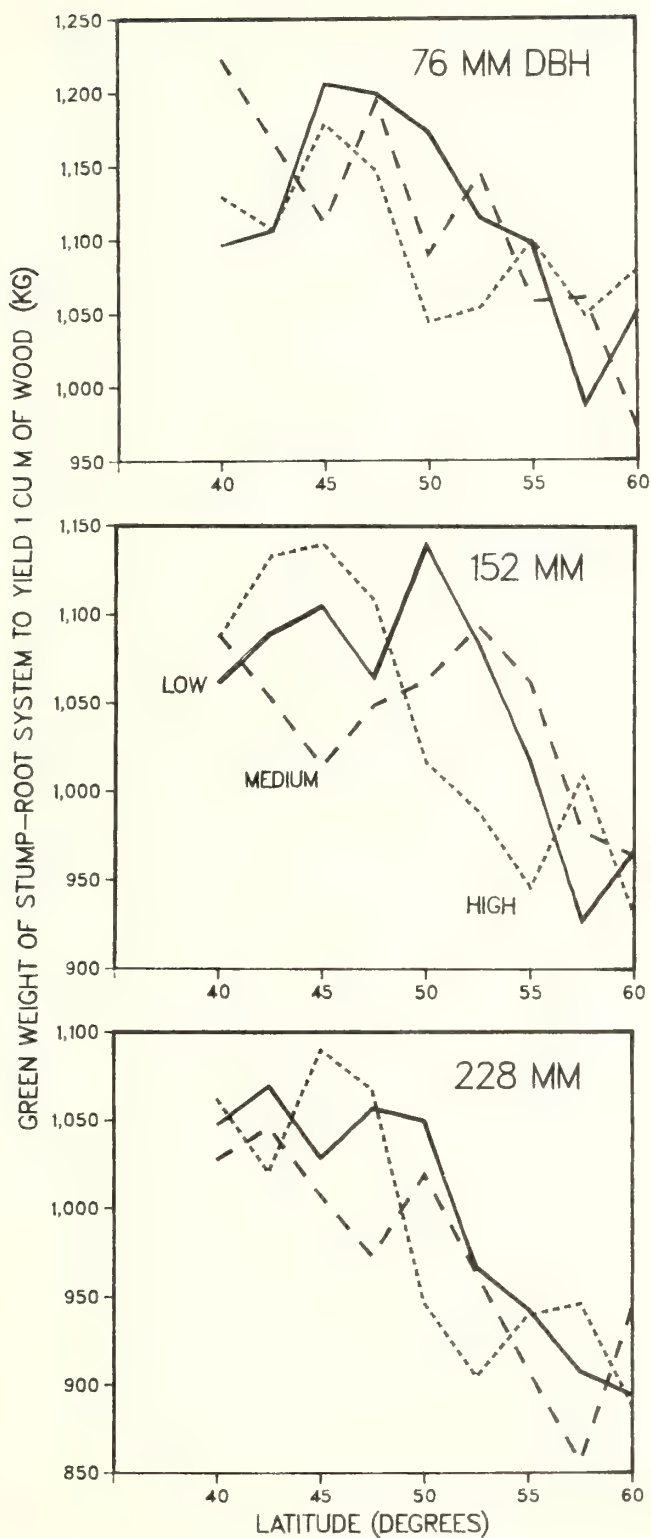


Figure 4-67—Green weight of stump-root systems, wood plus bark, required to yield 1 m³ of bark-free wood from *latifolia* trees of three diameters related to latitude and elevational zone.

Tree Component Proportion, Green-Weight Basis—

With all data pooled, wood plus bark of stump-root systems averaged 11.55 percent of green complete-tree weight including foliage, with standard deviation of 2.53 percentage points. This percentage was unrelated to elevational zone but was negatively correlated with d.b.h. (fig. 4-68), averaging 13.54 (2.67), 11.19 (1.70), and 9.93 (1.60) percent for trees 76, 152, and 228 mm in d.b.h.

In 76-mm trees the percentage increased in northerly latitudes, but in the two larger diameter classes it declined slightly (fig. 4-68).

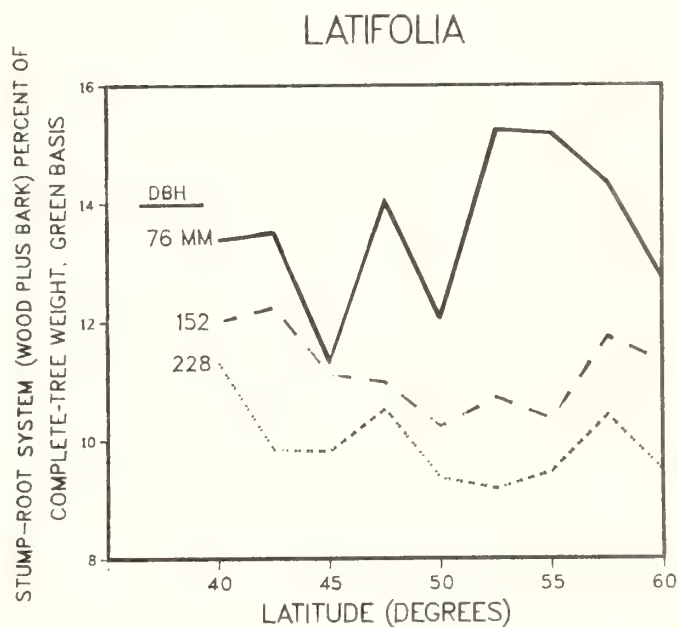


Figure 4-68—Stump-root system (wood plus bark) as percentage of complete-tree weight including foliage—green basis—of *latifolia* trees of three diameters related to latitude.

Tree Component Proportion, Ovendry-Weight Basis—

On an ovendry basis, wood plus bark of the stump-root system averaged 11.57 percent of complete-tree weight including foliage, with standard deviation of 2.44 percentage points. This percentage was unrelated to elevational zone but was negatively correlated with d.b.h. (fig. 4-69), averaging 13.33 (2.64), 11.39 (1.67), and 9.98 (1.60) for trees 76, 152, and 228 mm in d.b.h.

Latitudinal trends (fig. 4-69) were similar to those for green-weight percentages.

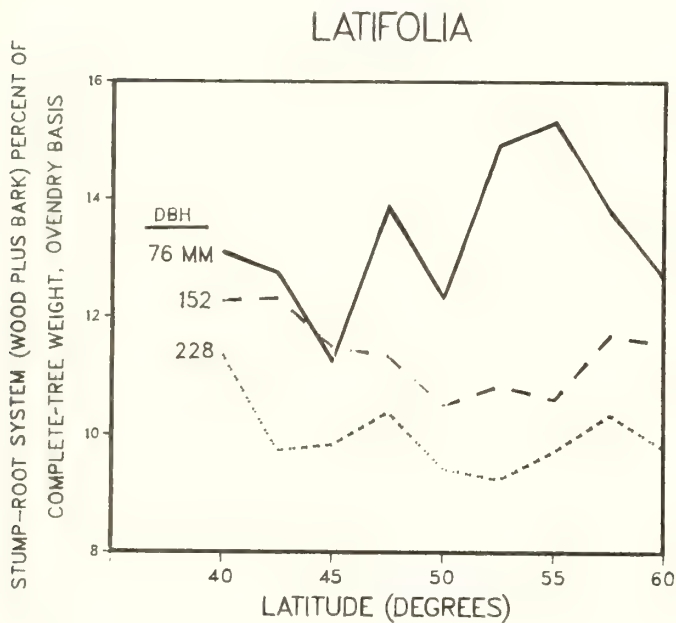


Figure 4-69—Stump-root system (wood plus bark) as percentage of complete-tree weight including foliage—ovendry basis—of *latifolia* trees of three diameters related to latitude.

Stump-Root System, Wood Only

Specific Gravity—Wood of the stump-root system had average specific gravity of 0.469, with standard deviation of 0.045, based on ovendry weight and green volume. Specific gravity was unrelated to elevational zone, but varied with latitude. Wood specific gravity was least (0.444) at 42.5 degrees and most (0.476 to 0.493) in latitudes 47.5 through 55 degrees. In northern latitudes, trees from low-elevation zones had higher specific gravity than those from high zones (fig. 4-70).

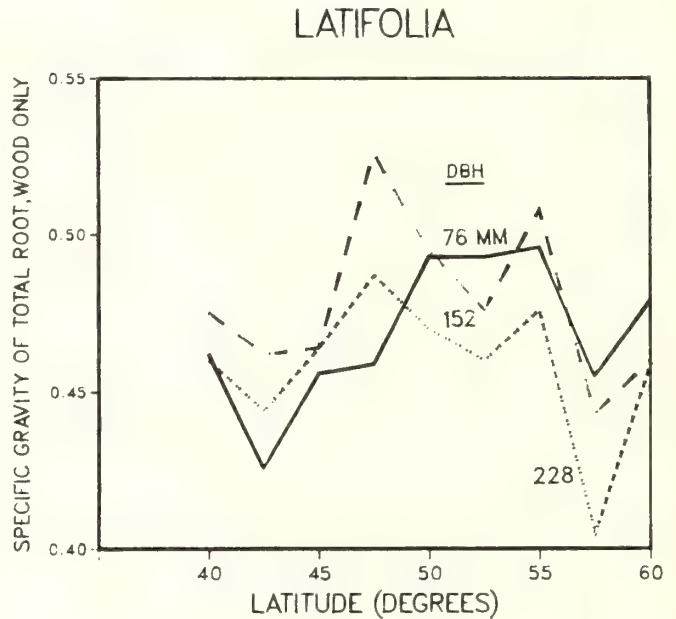


Figure 4-70—Specific gravity (based on ovendry weight and green volume) of wood of stump-root systems of *latifolia* trees of three diameters related to latitude.

Weight, Green—Green weight of wood from the stump-root system was positively correlated with d.b.h., averaging 3.19 (0.76), 16.53 (2.79), and 38.67 (6.29) kg for trees 76, 152, and 228 mm in d.b.h. This weight was inversely correlated with elevational zone, averaging—with diameter data pooled—20.35, 19.54, and 18.50 kg for low-, medium-, and high-elevation zones, respectively; interactions with diameter and latitude were complex, however (fig. 4-71). In low-elevation zones, green weights were greatest in southern latitudes and least in northern latitudes (fig. 4-71)—partly attributable to a similar trend in root-wood moisture content with latitude (fig. 2-24).

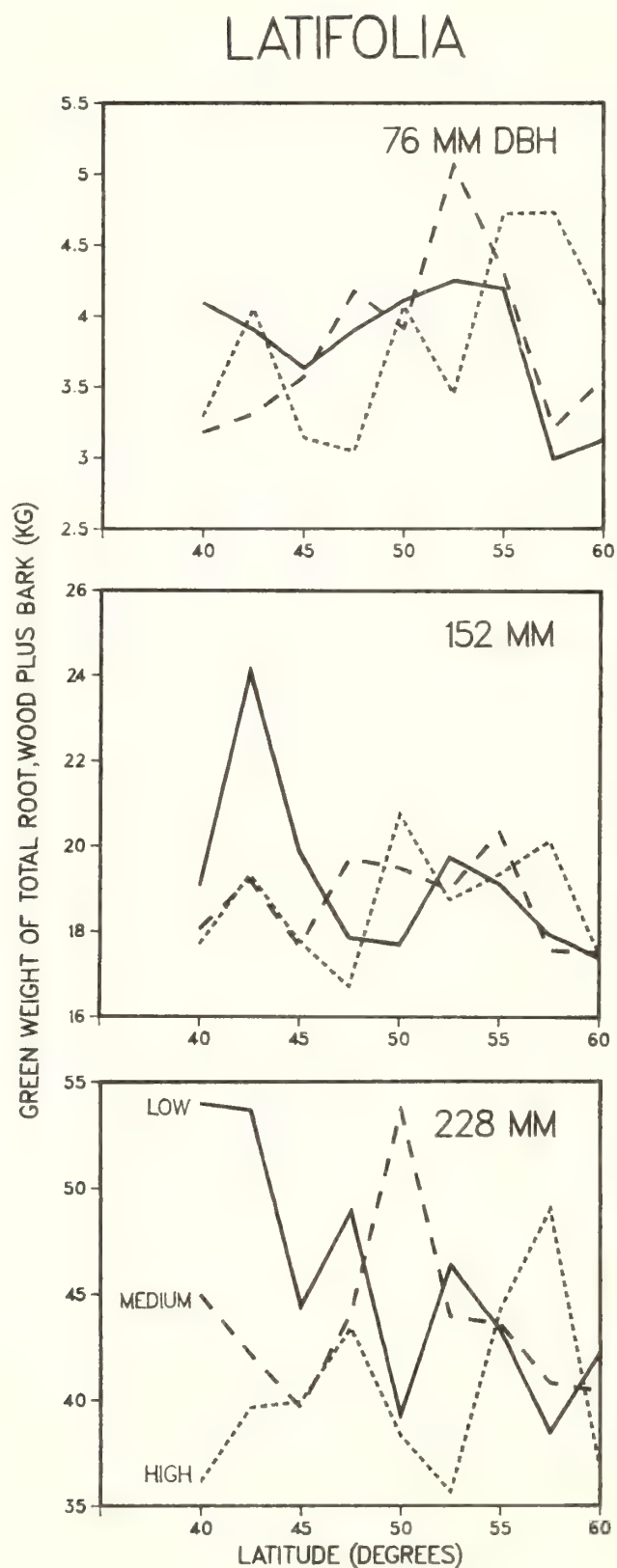


Figure 4-71—Green weight of wood from the stump-root systems of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis, weight of wood of the stump-root system tended to be least (9.2 to 9.8 kg with diameter data pooled) in the southern three latitudinal zones, and most in the latitudes from 47.5 through 55 degrees (10.4 to 11.4 kg with diameter data pooled). In larger trees, rootwood from high-elevation zones weighed slightly less than that from low zones (fig. 4-72).

Ovendry rootwood weight was positively correlated with d.b.h., averaging 1.62 (0.39), 8.66 (1.51), and 20.13 (3.06) kg for trees of the three diameter classes.

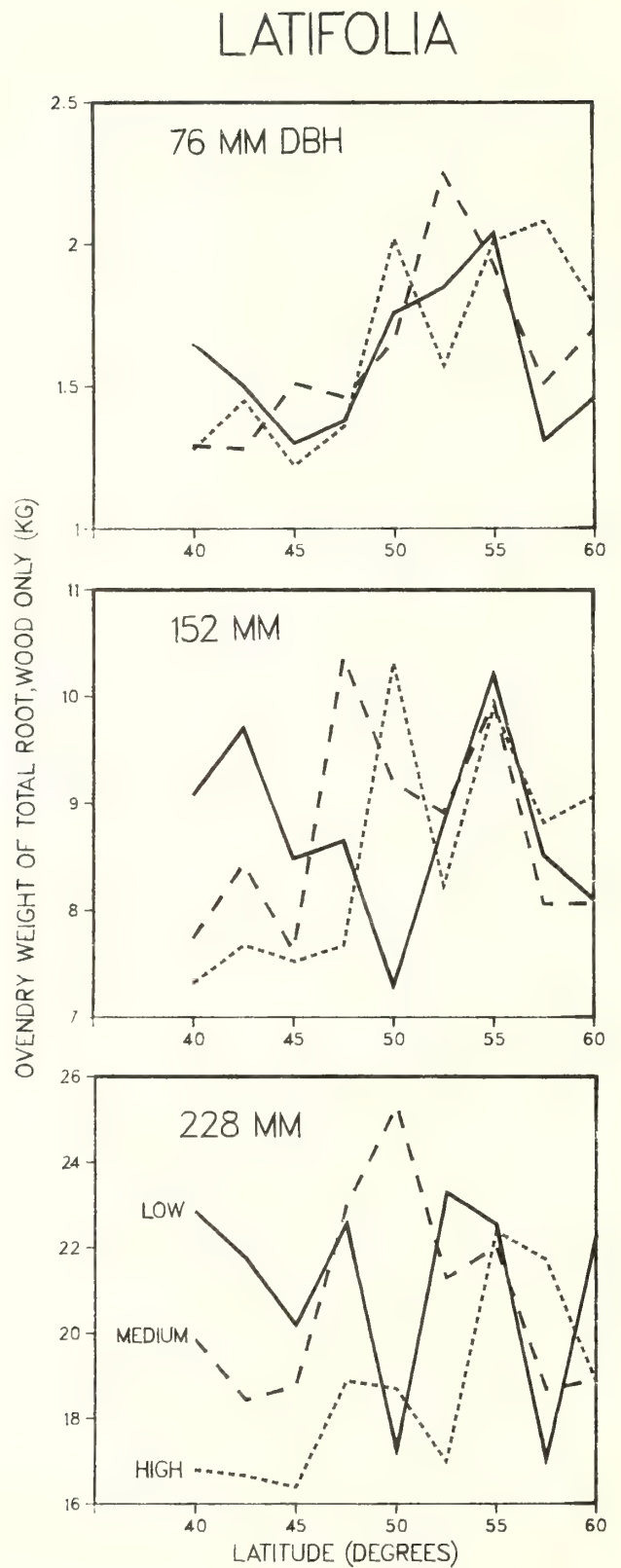


Figure 4-72—Ovendry weight of wood from the stump-root systems of *latifolia* trees of three diameters related to latitude and elevational zone.

Stump-Root System, Bark Only

Specific Gravity—Specific gravity of bark of the stump-root system was higher than that of stembark or branch-bark (table 4-2), averaging 0.415, with standard deviation of 0.056, based on oven-dry weight and green volume. It was positively correlated with d.b.h., averaging 0.393 (0.054), 0.419 (0.057), and 0.435 (0.051) for trees 76, 152, and 228 mm in d.b.h.

Rootbark specific gravity was negatively correlated with elevational zone, averaging 0.425, 0.417, and 0.403 in low, medium, and high zones (fig. 4-73); this relationship was weakest in small trees. Specific gravity averaged least (0.358) at 42.5 degrees latitude and most (0.442 to 0.450) in latitudinal zones from 50 through 55 degrees (fig. 4-73).

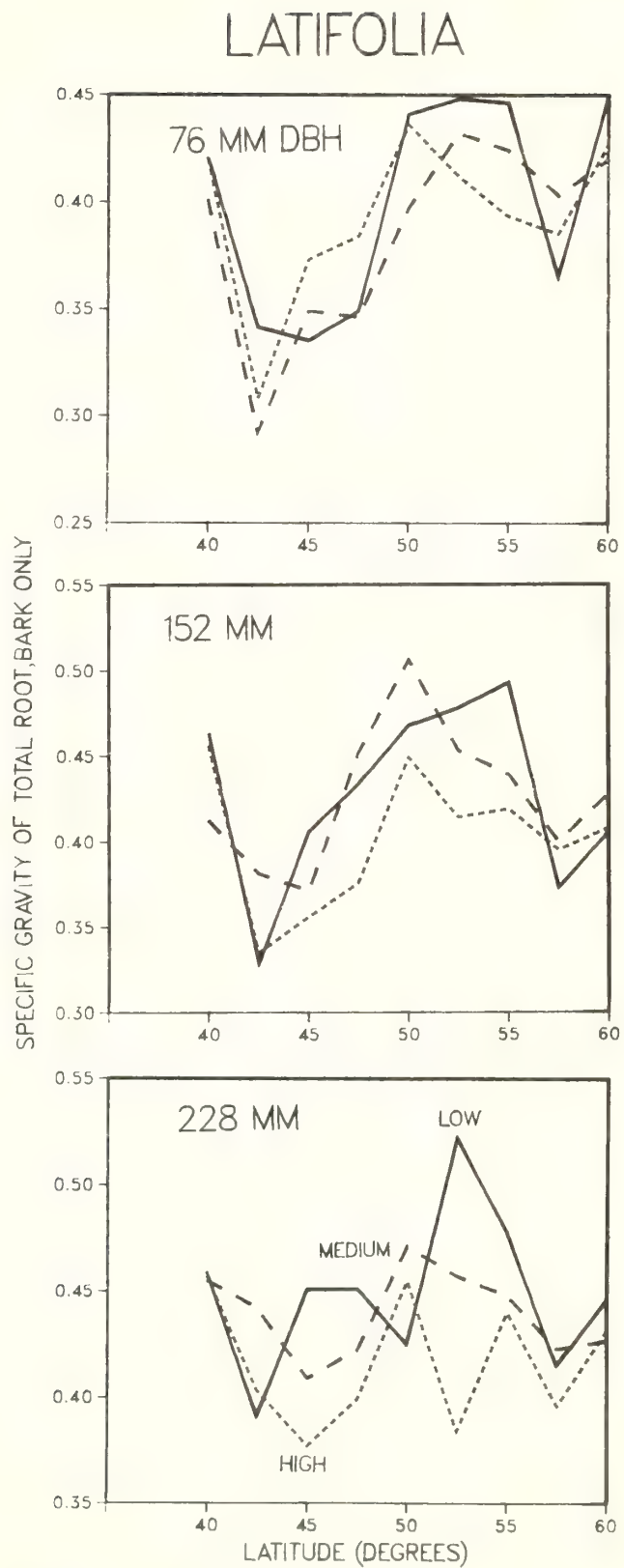


Figure 4-73—Specific gravity (based on oven-dry weight and green volume) of bark from the stump-root systems of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Green—Green weight of bark of the stump-root system was positively correlated with d.b.h., averaging 0.63 (0.19), 2.33 (0.68), and 4.54 (1.05) kg for trees of the three diameter classes. It was unrelated to elevational zone. For the smaller trees, root-system green bark weighed more in northern latitudes than southern (fig. 4-74).

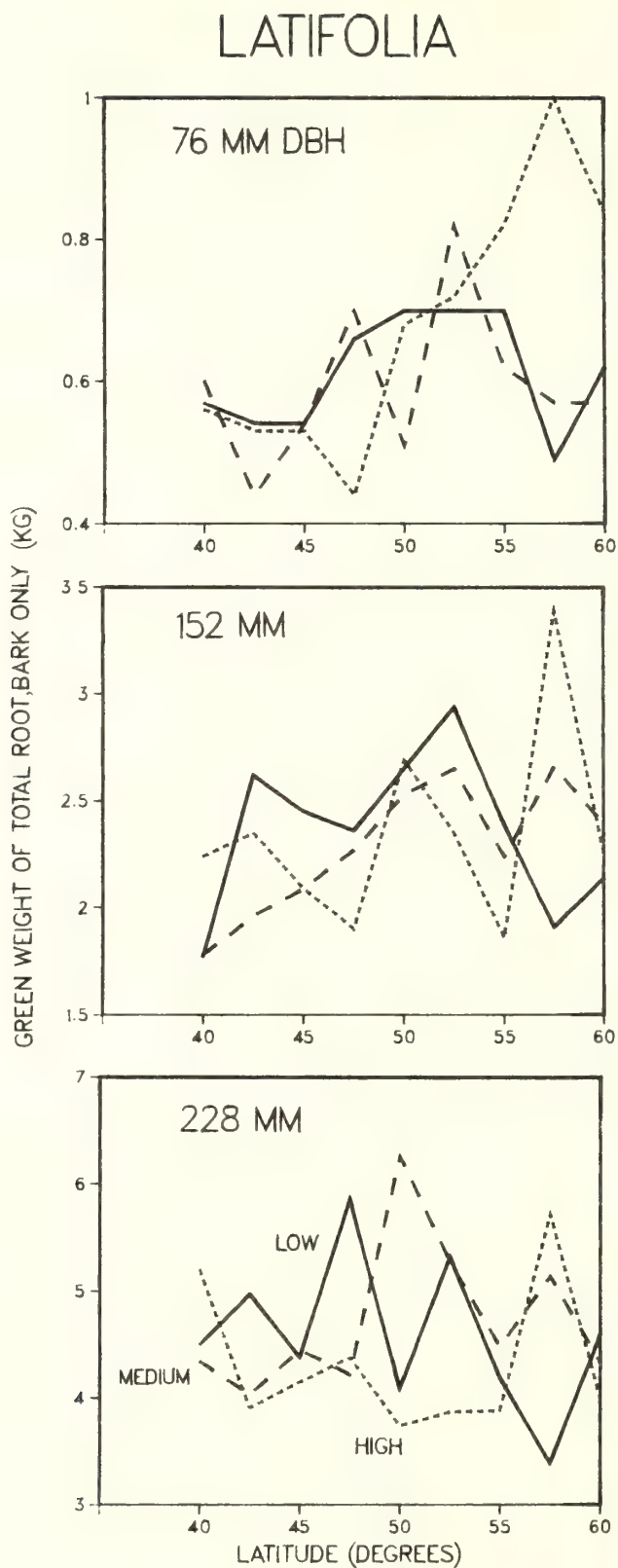


Figure 4-74—Green weight of bark from the stump-root systems of *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis, average weight of the stump-root system bark was lowest—diameter data pooled—at 42.5 degrees latitude (1.04 kg) and highest (1.42 to 1.45 kg) at 50 and 52.5 degrees (fig. 4-75). In the middle latitudes, trees from high-elevation zones had less weight of root-system bark than those from low zones (fig. 4-75).

Weight of ovendry bark of the stump-root system was positively correlated with d.b.h., averaging 0.30 (0.10), 1.17 (0.35), and 2.30 (0.60) kg for trees 76, 152, and 228 mm in d.b.h.

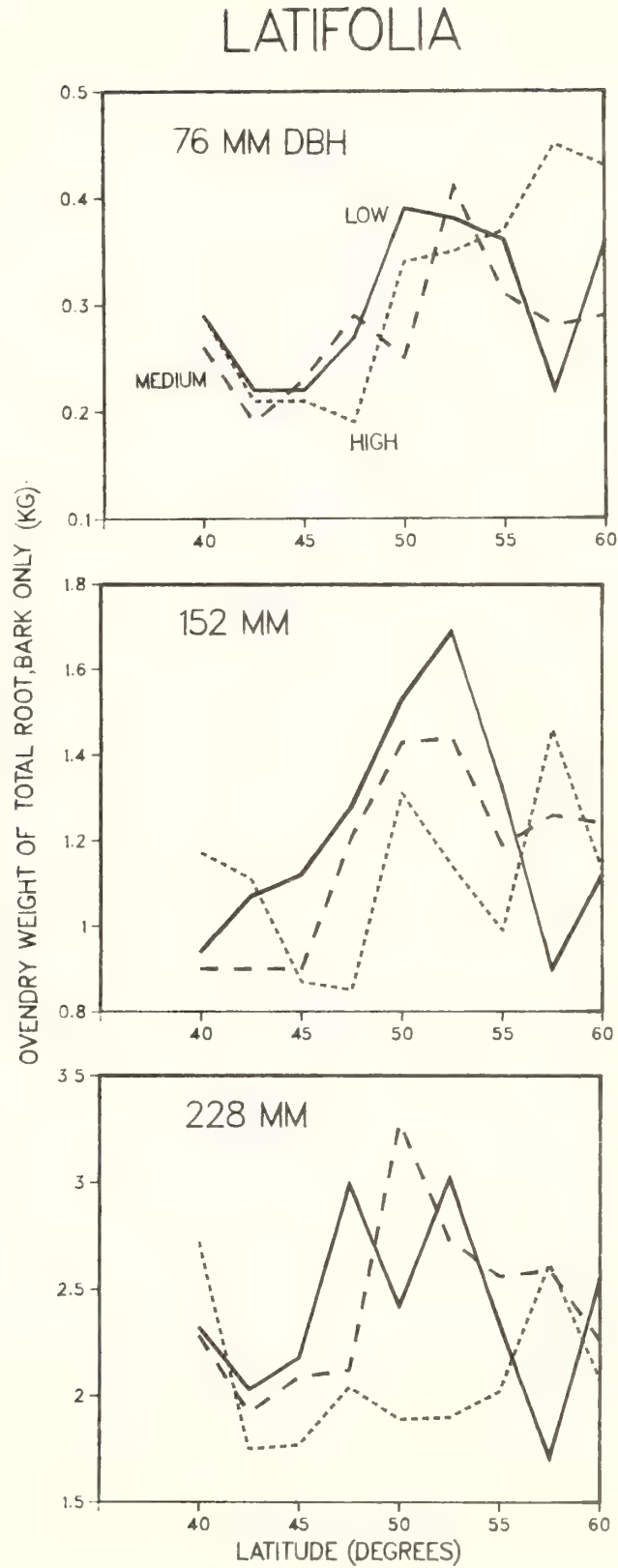


Figure 4-75—Ovendry weight of bark from the stump-root systems of *latifolia* trees of three diameters related to latitude and elevational zone.

Stump-Root Bark as Percentage of Gross Stump-Root Weight, Green and Ovendry—On a green-weight basis, bark of stump-root systems averaged 13.13 percent of gross stump-root system weight, with standard deviation of 3.72 percentage points. On an ovendry-weight basis, comparable values were 12.52 (3.52) percent. Average percentage of bark by weight, both green and ovendry, was lowest at 42.5 degrees latitude (11.35 and 10.88 percent, respectively) and highest at 52.5 degrees (14.37 and 14.01 percent); elevational trends were complex, and varied with latitude and d.b.h. (figs. 4-76 and 4-77).

Bark weight percentages were negatively correlated with d.b.h., as follows:

D.b.h.	Green	Ovendry
mm	Percent	
76	16.51 (3.32)	15.46 (3.21)
152	12.32 (2.83)	11.85 (2.96)
228	10.55 (1.99)	10.25 (2.02)

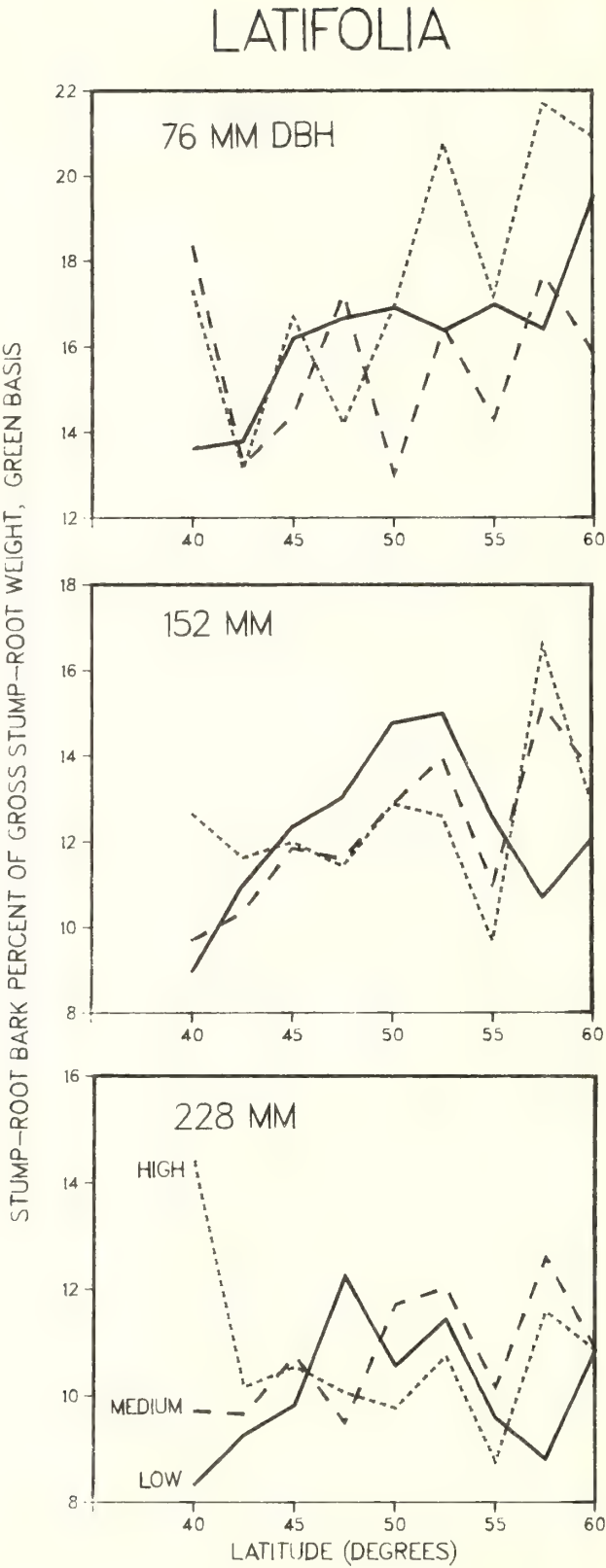


Figure 4-76—Weight of stump-root system bark as a percentage of gross stump-root systems (green basis) of *latifolia* trees of three diameters related to latitude and elevational zone.

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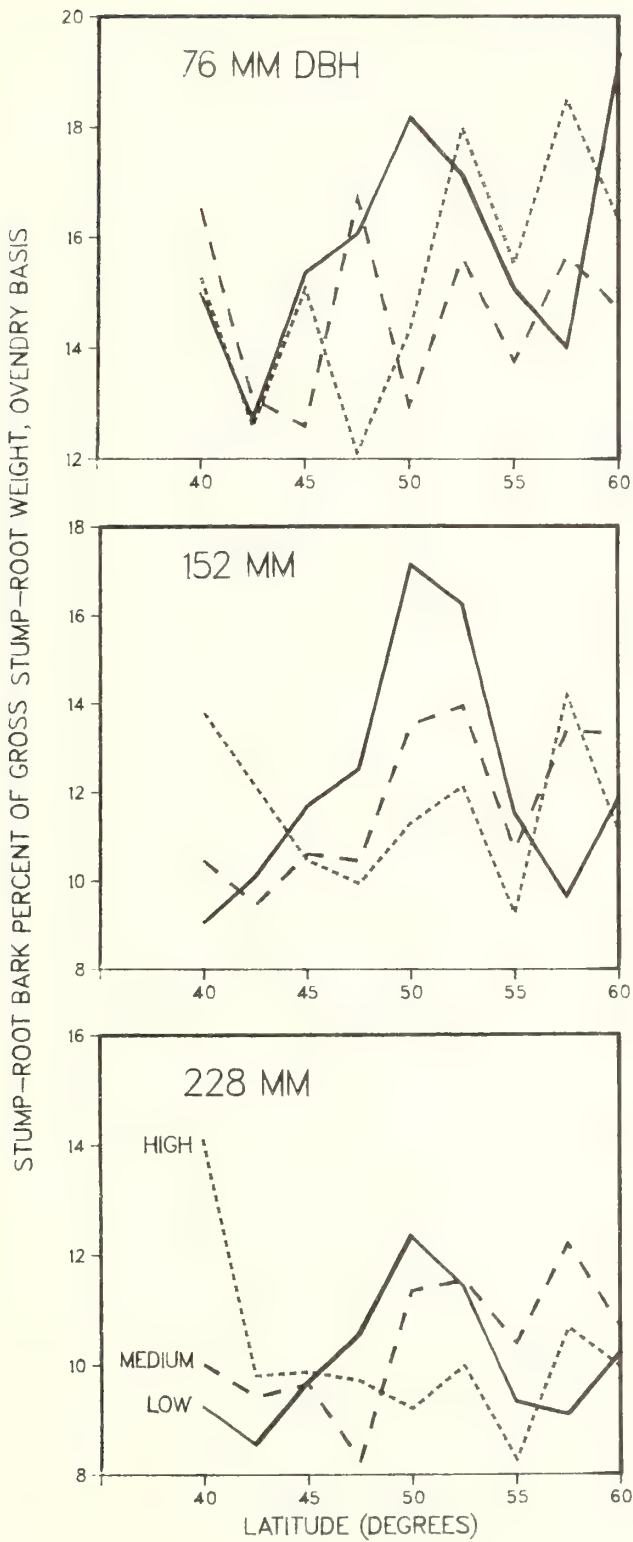


Figure 4-77—Weight of stump-root system bark as a percentage of gross stump-root systems (ovendry basis) of *latifolia* trees of three diameters related to latitude and elevational zone.

Stump, Wood Plus Bark

Specific Gravity—Wood plus bark of the stumps had higher specific gravity than wood plus bark of any other tree component (table 4-2), averaging 0.471, with standard deviation of 0.046, based on oven-dry weight and green volume. Specific gravities were highest in the smaller trees, averaging 0.475 (0.047), 0.480 (0.048), and 0.459 (0.041) in trees 76, 152, and 228 mm in d.b.h.

Specific gravities averaged least (0.443) at 42.5 degrees latitude and most at 52.5 and 55 degrees (0.494 and 0.492, respectively); variations with elevation were complex and differed with latitude (fig. 4-78).

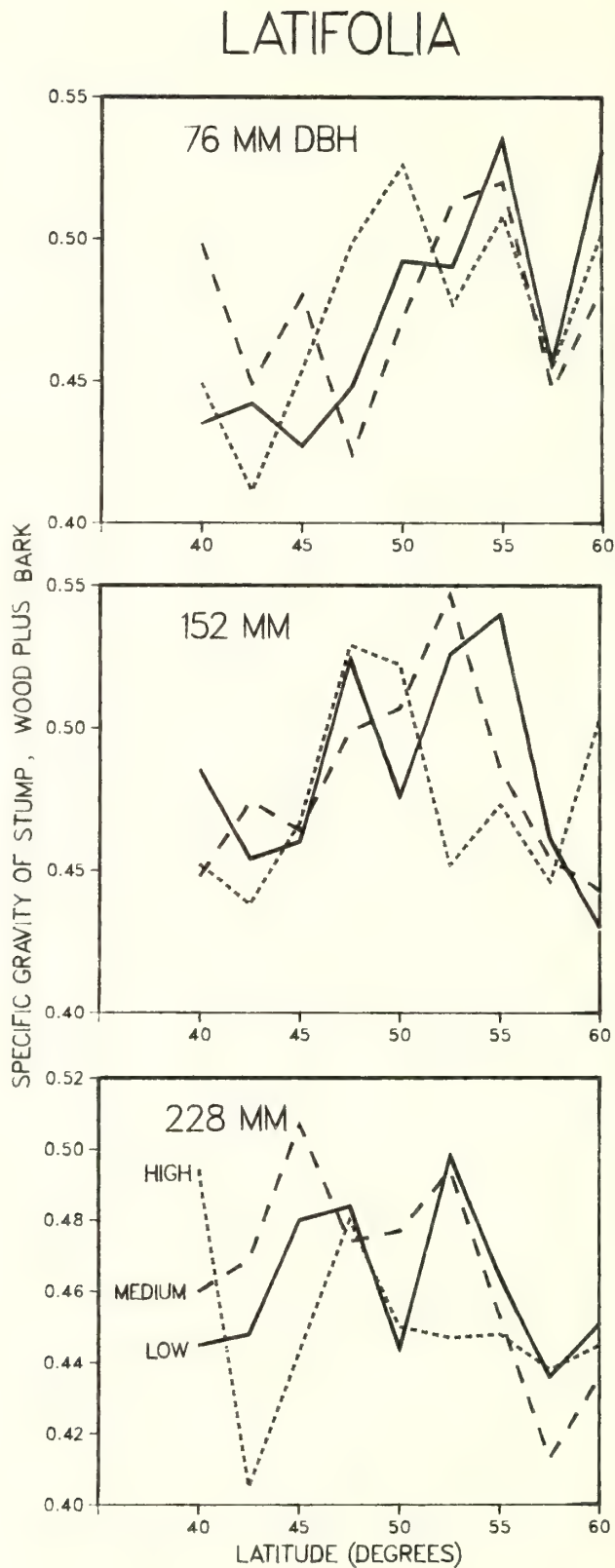


Figure 4-78—Specific gravity (based on oven-dry weight and green volume) of wood plus bark of stumps from ground level to 152-mm height from *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Green—Weight of green wood plus bark of stumps was positively correlated with d.b.h. (fig. 4-79), averaging 1.15 (0.32), 3.67 (1.24), and 7.18 (2.54) kg for trees 76, 152, and 228 mm in d.b.h. Weight was unrelated to elevational zone, but was negatively correlated with latitude, particularly in smaller trees (fig. 4-79).

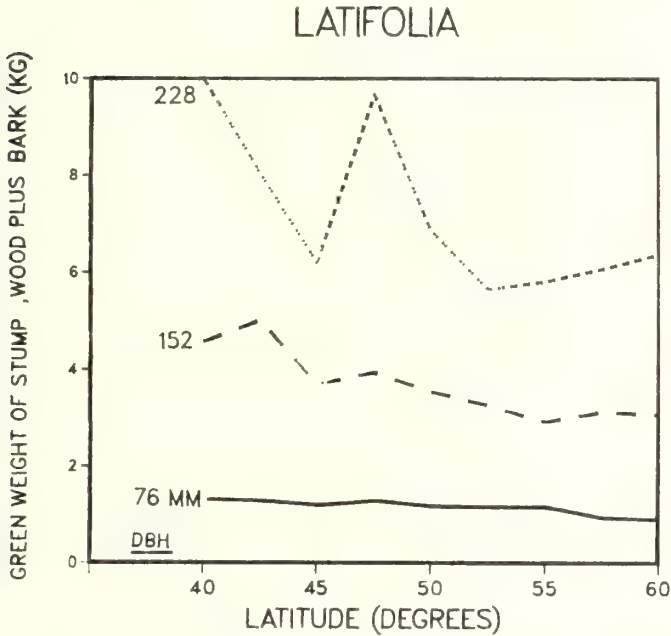


Figure 4-79—Green weight of wood plus bark of stumps (ground level to 152-mm stump height) from *latifolia* trees of three diameters related to latitude.

Weight, Ovendry—Ovendry weights of wood plus bark of stumps were also unrelated to elevational zone but positively correlated with d.b.h. (fig. 4-80), averaging 0.59 (0.14), 2.01 (0.61), and 3.89 (1.31) kg for trees of the three diameter classes. Weights, ovendry, in northern latitudes were slightly less than those in southern (fig. 4-80).

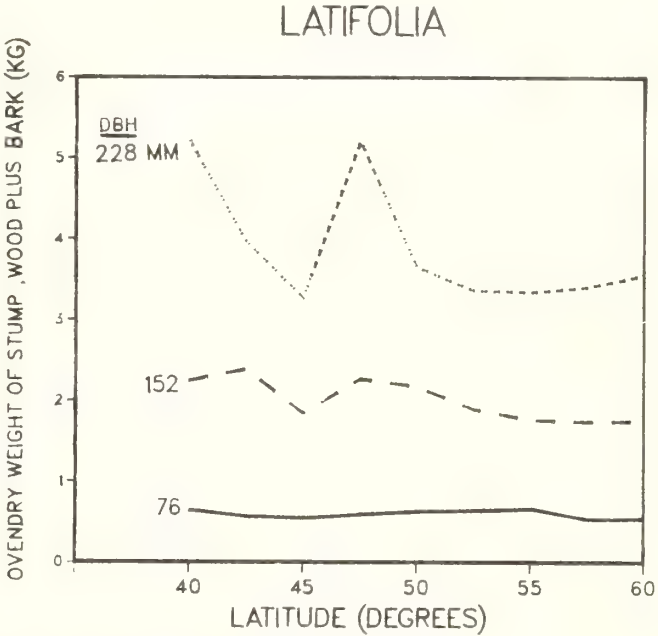


Figure 4-80—Ovendry weight of wood plus bark of stumps (ground level to 152-mm stump height) from *latifolia* trees of three diameters related to latitude.

Stumpwood

Specific Gravity—Stumpwood had specific gravity averaging 0.476, with standard deviation of 0.051, based on oven-dry weight and green volume. It was highest in smaller trees, averaging 0.486 (0.051), 0.485 (0.052), and 0.457 (0.044) in trees 76, 152, and 228 mm in d.b.h. This inverse relationship to d.b.h. is unusual in conifers.

Stumpwood specific gravity averaged minimum (0.447) at 42.5 degrees latitude and was maximum (0.486 to 0.498) from 47.5 degrees through 55 degrees; its relationship to elevation was not pronounced and varied with latitude (fig. 4-81).

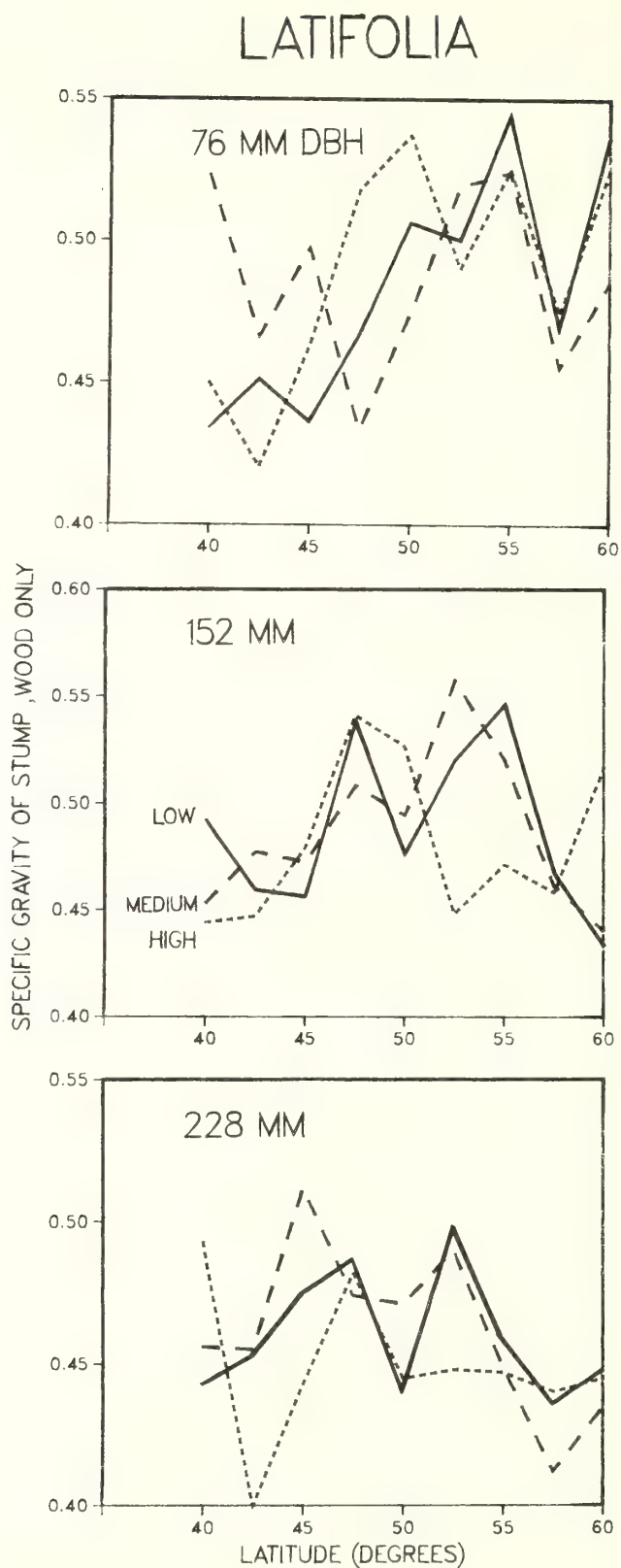


Figure 4-81—Specific gravity of stumpwood (based on oven-dry weight and green volume) from *latifolia* trees of three diameters related to latitude and elevational zone.

Weight, Green—Stumpwood green weight was unrelated to elevational zone, but positively correlated with d.b.h. (fig. 4-82), averaging 0.98 (0.28), 3.28 (1.06), and 6.51 (2.25) kg for trees 76, 152, and 228 mm in d.b.h. Trees in northern latitudes, particularly small trees, had less weight of green stumpwood than trees in southern latitudes (fig. 4-82).

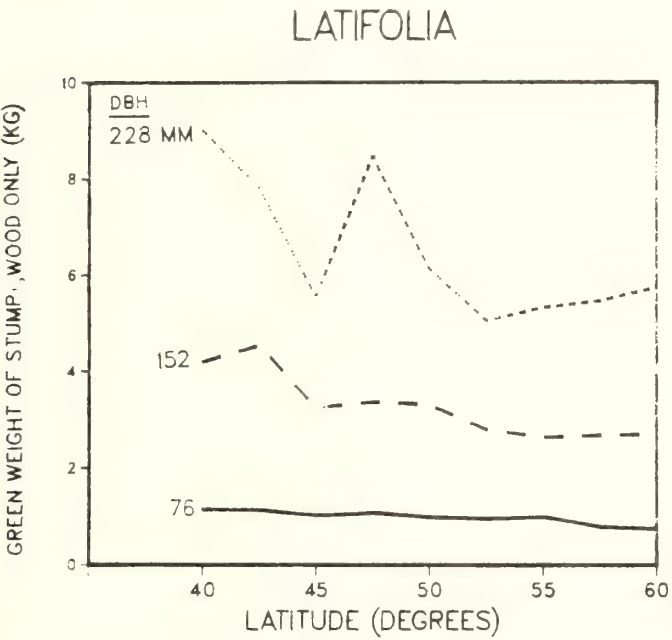


Figure 4-82—Green weight of stumpwood, from groundline to 152-mm stump height, of *latifolia* trees of three diameters related to latitude.

Weight, Ovendry—Weight of ovendry stumpwood was also unrelated to elevational zone, but positively correlated with d.b.h. (fig. 4-83), averaging 0.50 (0.12), 1.76 (0.54), and 3.45 (1.15) kg for trees of the three diameter classes. As with green stumpwood, ovendry weights in northern latitudes were slightly less than those in southern latitudes (fig. 4-83).

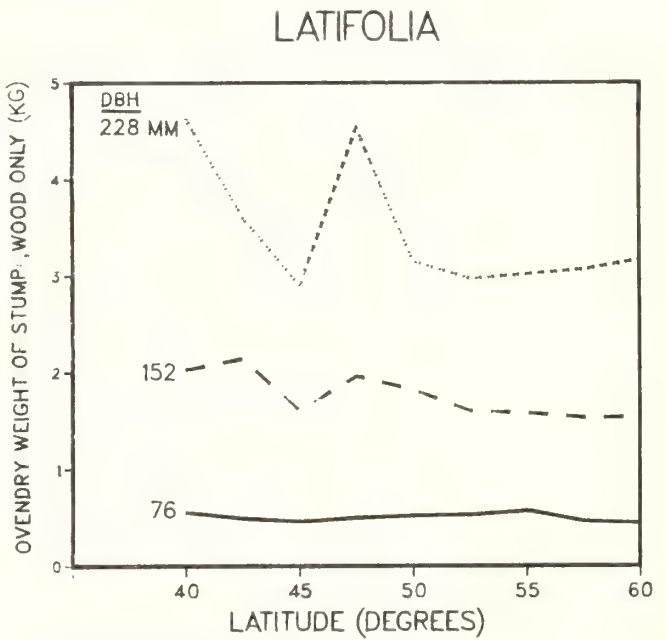


Figure 4-83—Ovendry weight of stumpwood, from groundline to 152-mm stump height, of *latifolia* trees of three diameters related to latitude.

Stumpbark

Specific Gravity—Stumpbark specific gravity was greater than that of the bark of any other tree component (table 4-2), averaging 0.445, with standard deviation of 0.064, based on oven-dry weight and green volume. Stumpbark specific gravity was unrelated to elevational zone. Unlike wood of stem and stump, specific gravity of stumpbark was positively correlated with d.b.h. (fig. 4-84), averaging 0.418 (0.063), 0.446 (0.068), and 0.470 (0.051) for trees 76, 152, and 228 mm in d.b.h.

It was also positively correlated with latitude, averaging minimum (0.401) at 42.5 degrees and maximum (0.486) at 50 degrees (fig. 4-84).

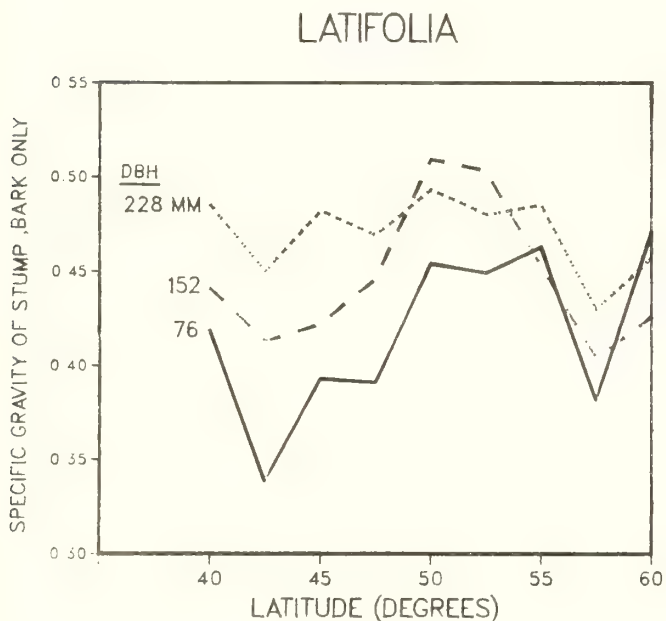


Figure 4-84—Specific gravity of stumpbark (based on oven-dry weight and green volume) from *latifolia* trees of three diameters related to latitude.

Weight, Green—Stumpbark green weight was positively correlated with d.b.h., averaging 0.17 (0.06), 0.43 (0.23), and 0.72 (0.36) kg for trees of the three diameter classes. Stumpbark tended to weigh most in low-elevation zones (fig. 4-85) and weight was minimum (0.31 kg) at 55 degrees latitude and maximum (0.65 kg) at 47.5 degrees (fig. 4-85).

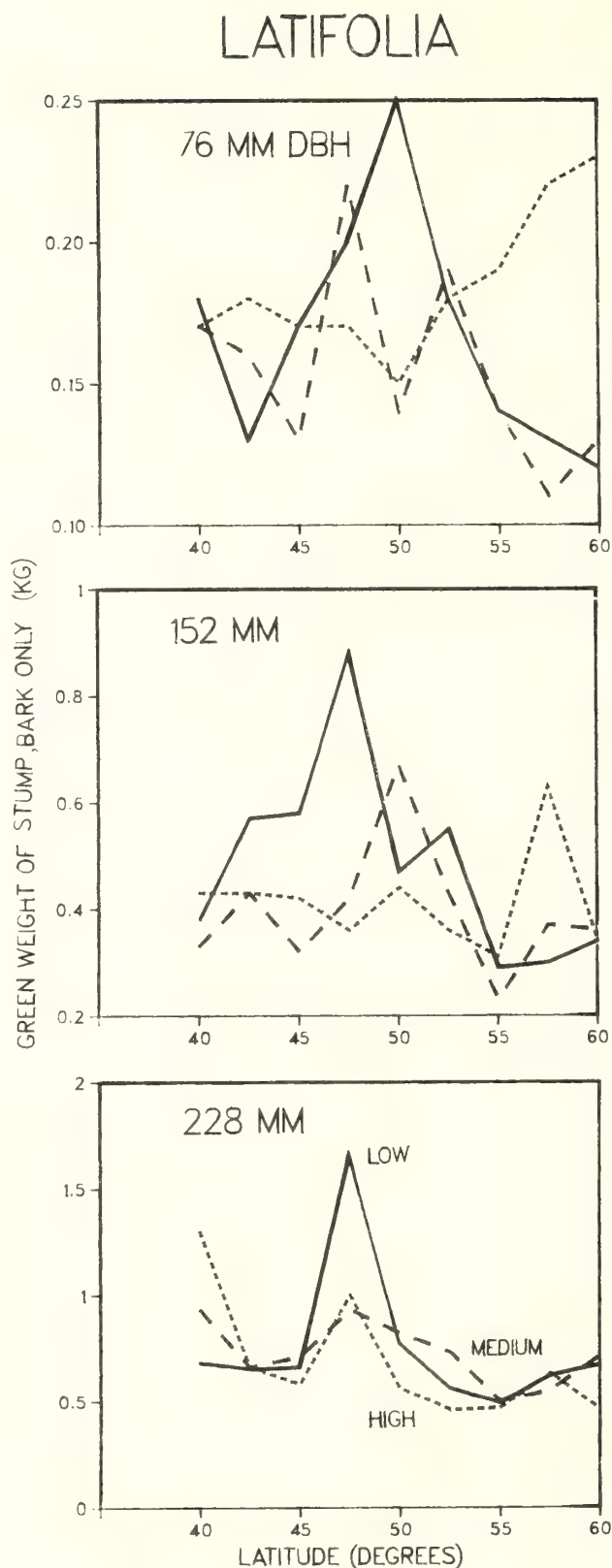


Figure 4-85—Green weight of stumpbark from groundline to 152-mm stump height of *latifolia* trees of three diameters, related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis, stumpbark weight was also positively correlated with d.b.h., averaging 0.09 (0.03), 0.25 (0.13), and 0.44 (0.22) kg for trees 76, 152, and 228 mm in d.b.h. Ovendry stumpbark weight varied inversely with elevational zone (fig. 4-86), averaging 0.28, 0.26, and 0.24 kg in low, medium, and high zones. As with green stumpbark, ovendry weight of stumpbark averaged minimum (0.19 kg) at 55 degrees latitude and was maximum (0.37 kg) at 47.5 degrees.

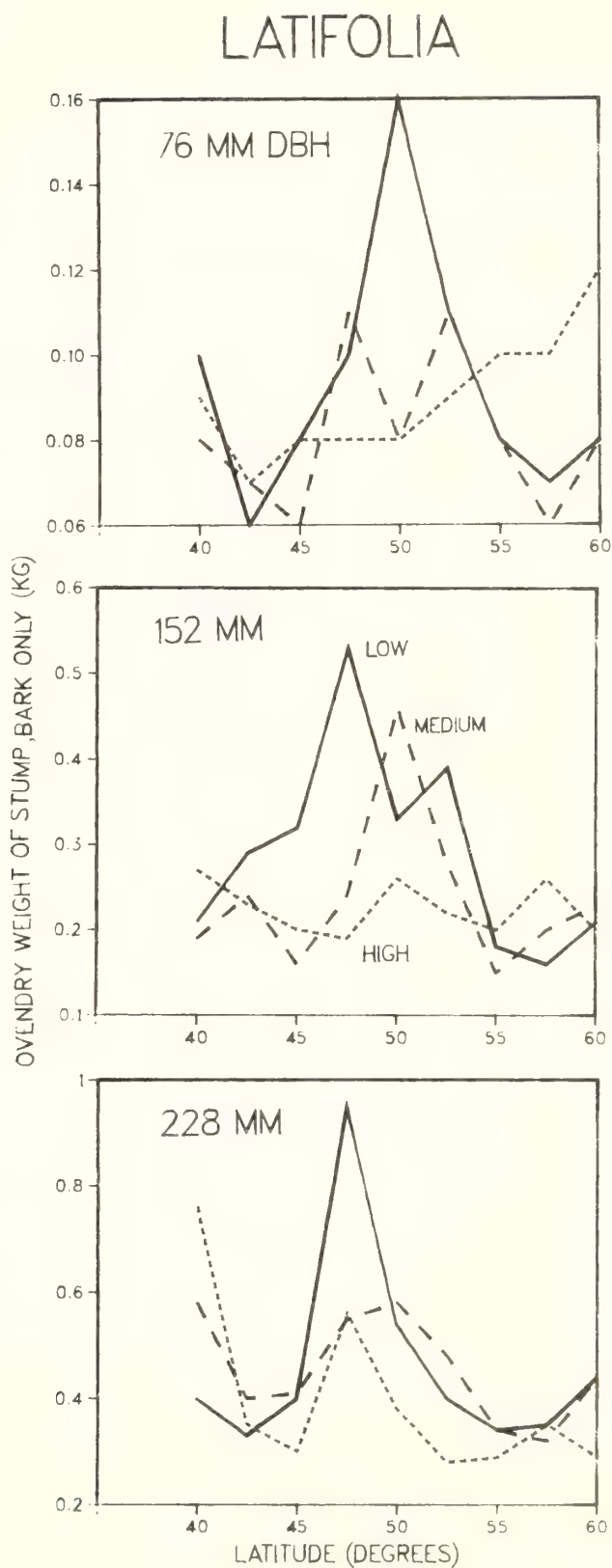


Figure 4-86—Ovendry weight of stumpbark from groundline to 152-mm stump height of *latifolia* trees of three diameters, related to latitude and elevational zone.

Lateral Roots, Wood Plus Bark

Specific Gravity—Specific gravity of wood plus bark of lateral roots averaged 0.442, with standard deviation of 0.047, based on oven-dry weight and green volume. It was unrelated to elevational zone, but in southern latitudes was positively correlated with d.b.h. (fig. 4-87); with data from all latitudes pooled, it averaged 0.424 (0.046), 0.452 (0.050), and 0.449 (0.039) for trees 76, 152, and 228 mm in d.b.h.

Specific gravity of wood plus bark from lateral roots was positively correlated with latitude, averaging minimum (0.410) at 42.5 degrees and maximum (0.479) at 55 degrees (fig. 4-87).

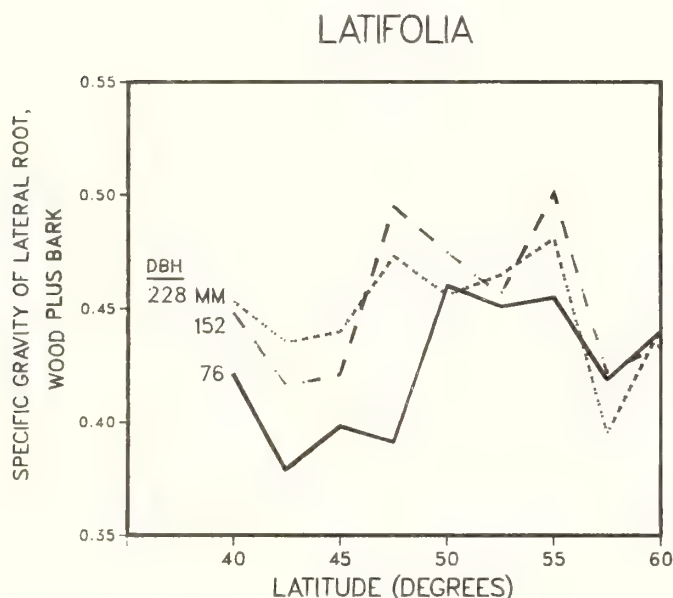


Figure 4-87—Specific gravity of wood plus bark (based on oven-dry weight and green volume) of lateral roots from root collar to 305-mm radius, from stump pith from *latifolia* trees of three diameters, related to latitude.

Weight, Green—Weight of green wood plus bark of lateral roots was unrelated to elevational zone, but positively correlated with d.b.h. (fig. 4-88), averaging 1.05 (0.52), 6.75 (1.70), and 15.52 (3.97) kg for trees of the three diameter classes. Unlike the stump, green weight of wood plus bark of the lateral roots was positively correlated with latitude, averaging near minimum (6.65 kg) at 40 degrees, minimum (6.19 kg) at 47.5 degrees, and maximum (9.24 kg) at 57.5 degrees (fig. 4-88).

Weight, Oven-dry—Weight of oven-dry wood plus bark of lateral roots was also unrelated to elevational zone, and positively correlated with d.b.h. (fig. 4-89), averaging 0.52 (0.28), 3.37 (0.96), and 7.80 (2.25) kg for trees of the three diameter classes. Oven-dry weight was positively correlated with latitude, averaging minimum (3.10 kg) at 40 degrees and maximum (4.84 kg) at 55 degrees (fig. 4-89).

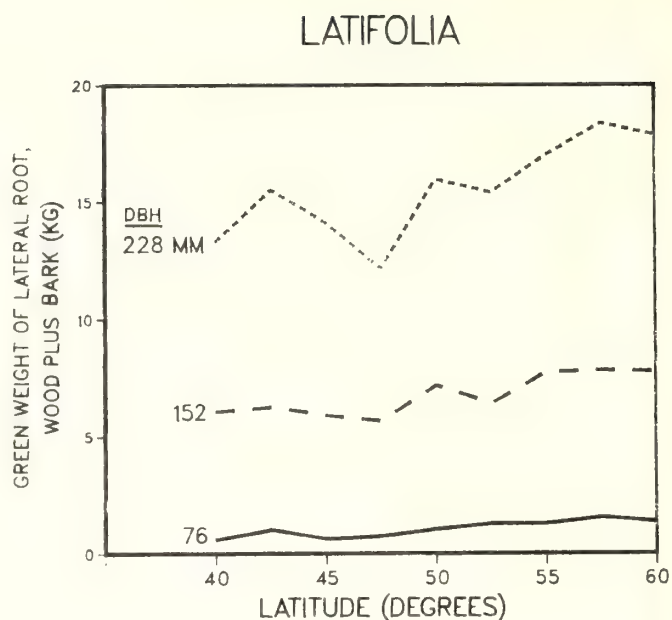


Figure 4-88—Green weight of wood plus bark from lateral roots (root collar to 305-mm radius from stump pith) of *latifolia* trees of three diameters, related to latitude.

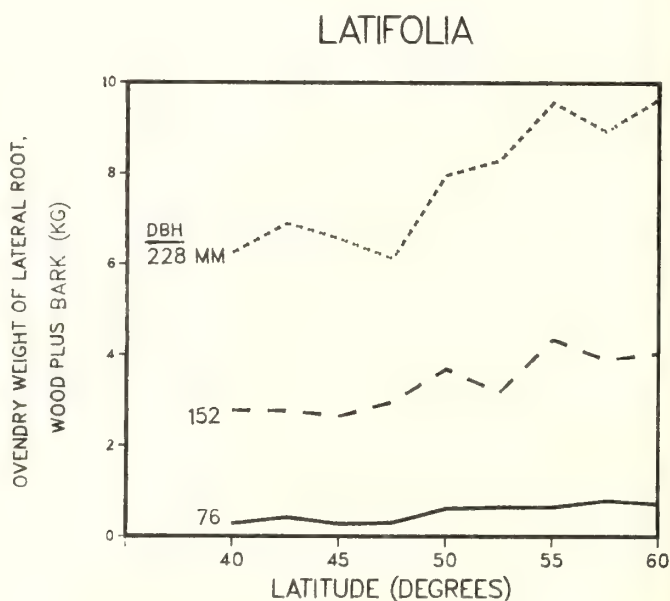


Figure 4-89—Oven-dry weight of wood plus bark from lateral roots (root collar to 305-mm radius from stump pith) of *latifolia* trees of three diameters, related to latitude.

Lateral Roots, Wood Only

Specific Gravity—Wood of the lateral roots had average specific gravity of 0.453, with standard deviation of 0.048, based on ovendry weight and green volume. It was unrelated to elevational zone and only in southern latitudes was positively correlated with d.b.h. (fig. 4-90). Specific gravity was lowest (0.427 and 0.421) at latitudes 42.5 and 57.5 degrees and highest (0.472) at middle latitudes of 47.5 and 50 degrees (fig. 4-90).

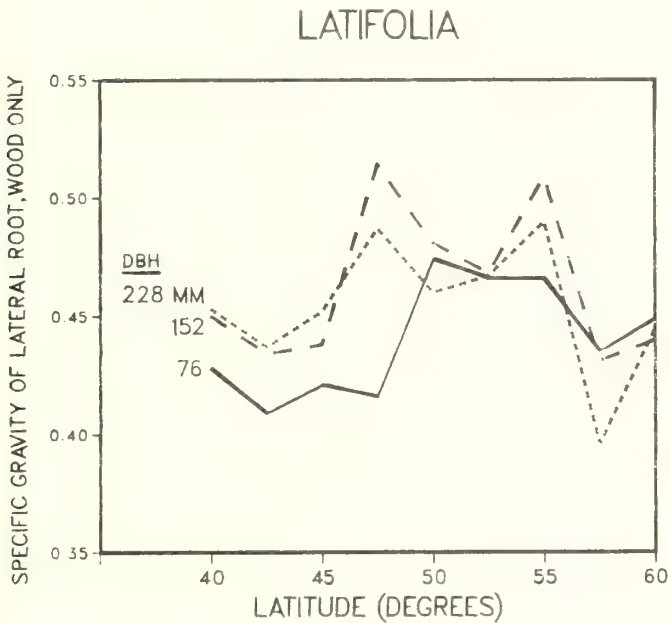


Figure 4-90—Specific gravity of wood of lateral roots (based on ovendry weight and green volume) of *latifolia* trees of three diameters, related to latitude.

Weight, Green—Weight of green wood from lateral roots was unrelated to elevational zone, but was positively correlated with d.b.h. (fig. 4-91), averaging 0.81 (0.43), 5.72 (1.46), and 13.45 (3.46) kg for trees 76, 152, and 228 mm in d.b.h. Weight of wood from lateral roots increased slightly from south to north, particularly in smaller trees (fig. 4-91).

Weight, Ovendry—On an ovendry basis the latitudinal trend was accentuated (fig. 4-92); with diameter data pooled, ovendry wood weight was minimum (2.66 kg) in the southernmost latitude of 40 degrees and maximum (4.25 and 4.15 kg) at 55 and 60 degrees.

As when green, ovendry weight was unrelated to elevational zone but positively correlated with d.b.h., averaging 0.40 (0.23), 2.88 (0.85), and 6.82 (1.97) kg for trees of the three diameter classes.

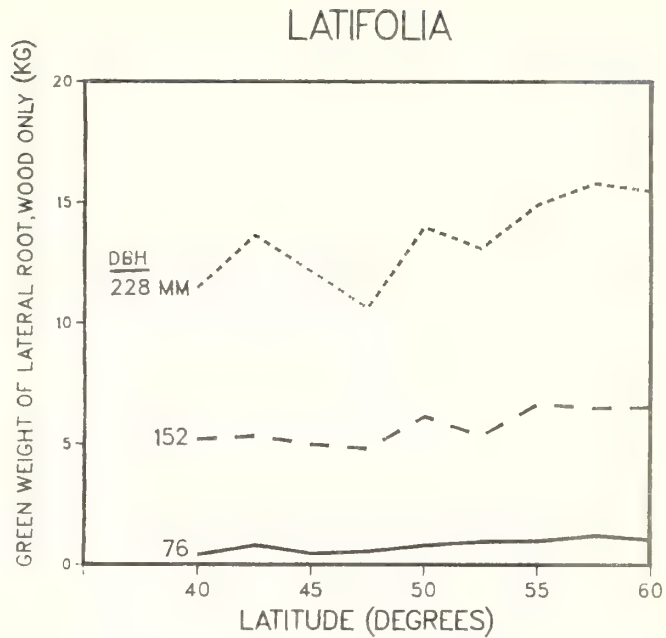


Figure 4-91—Green weight of wood of lateral roots (from root collar to 305-mm radius from stump pith) of *latifolia* trees of three diameters, related to latitude.

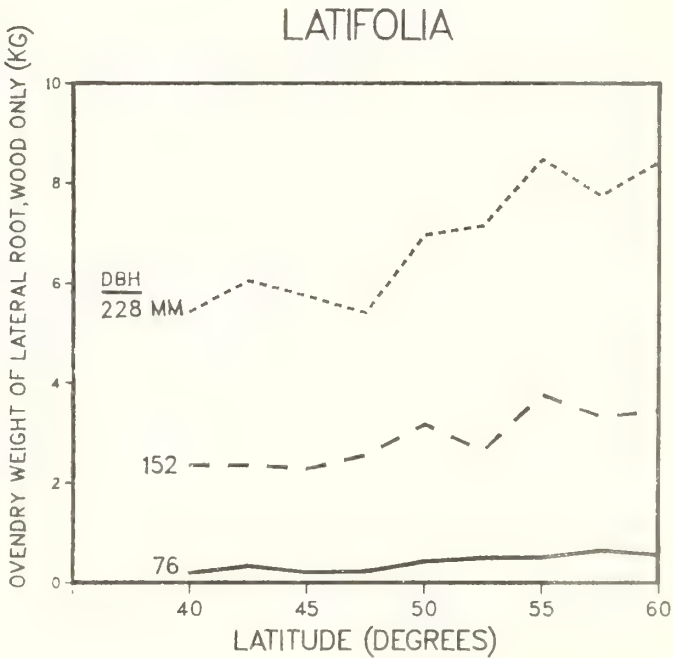


Figure 4-92—Ovendry weight of wood of lateral roots (from root collar to 305-mm radius from stump pith) of *latifolia* trees of three diameters, related to latitude.

Lateral Roots, Bark Only

Specific Gravity—Specific gravity of bark of lateral roots averaged 0.399, with standard deviation of 0.082, based on oven-dry weight and green volume. Specific gravity was unrelated to elevational zone, but in most latitudes it was positively correlated with d.b.h. (fig. 4-93), averaging 0.375 (0.070), 0.400 (0.076), and 0.421 (0.093) for trees 76, 152, and 228 mm in d.b.h. Except for latitude 40 degrees, where specific gravity averaged 0.440, it was positively correlated with latitude with minimum (0.346) at 45 degrees and a second maximum (0.435) at 55 degrees (fig. 4-93).

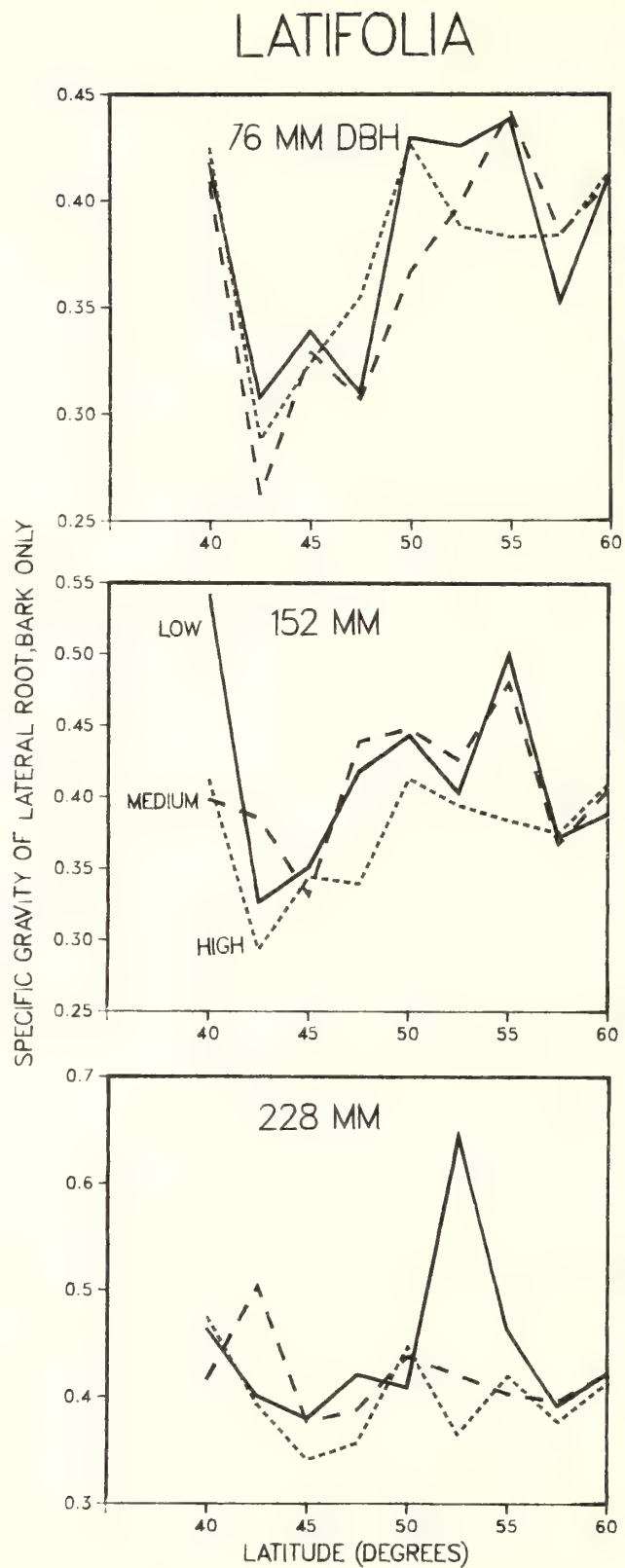


Figure 4-93—Specific gravity of bark of lateral roots (based on oven-dry weight and green volume) from *latifolia* trees of three diameters, related to latitude and elevational zone.

Weight, Green—With some variations (notably a minimum at 47.5 degrees), green weight of bark of lateral roots was positively correlated with latitude (fig. 4-94). Trees in low-elevation zones averaged less weight of such bark (1.08 kg) than those in high zones (1.16 kg).

Green weight of bark of lateral roots was positively correlated with d.b.h., averaging 0.24 (0.11), 1.03 (0.34), and 2.08 (0.65) kg for trees 76, 152, and 228 mm in d.b.h.

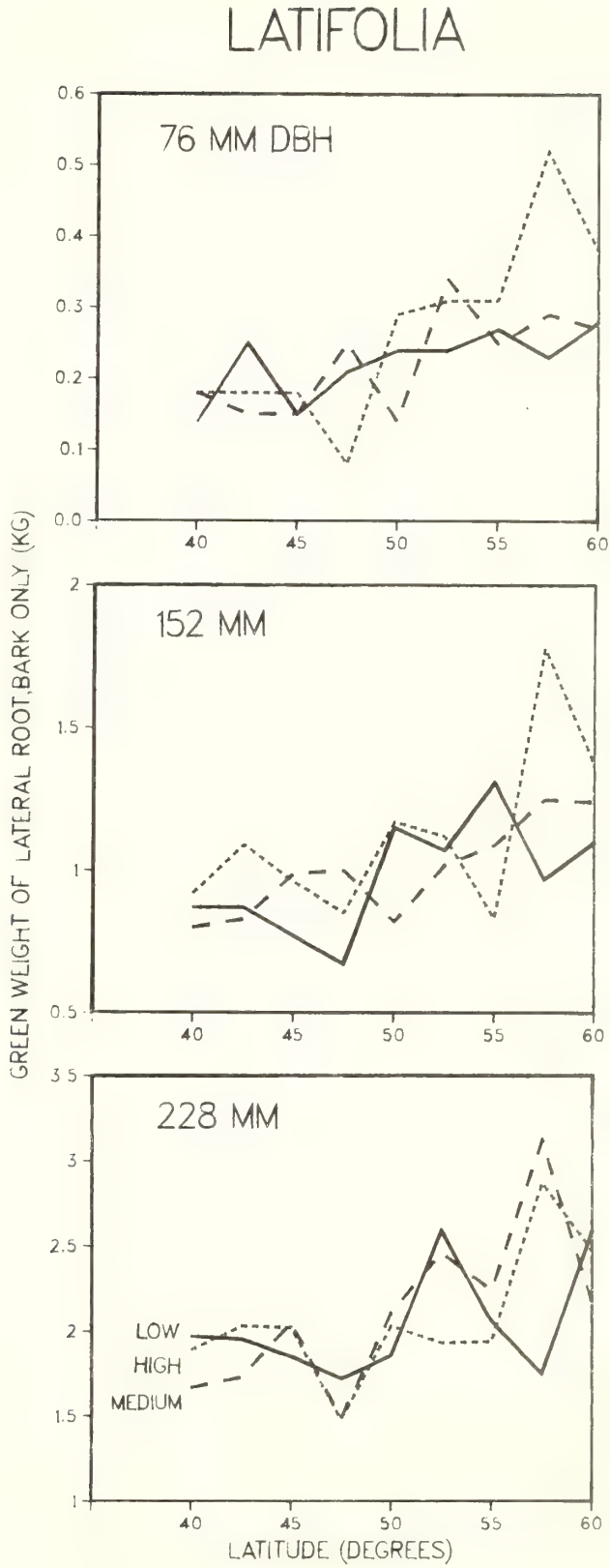


Figure 4-94—Green weight of bark of lateral roots from *latifolia* trees of three diameters, related to latitude and elevational zone.

Weight, Ovendry—On an ovendry basis, weight of bark of lateral roots decreased from 40 through 47.5 degrees latitude, and then increased with increasing latitude (fig. 4-95). It was unrelated to elevational zone.

Ovendry weight of lateral rootbark was positively correlated with d.b.h., averaging 0.11 (0.05), 0.49 (0.17), and 0.99 (0.33) kg for trees of the three diameter classes.

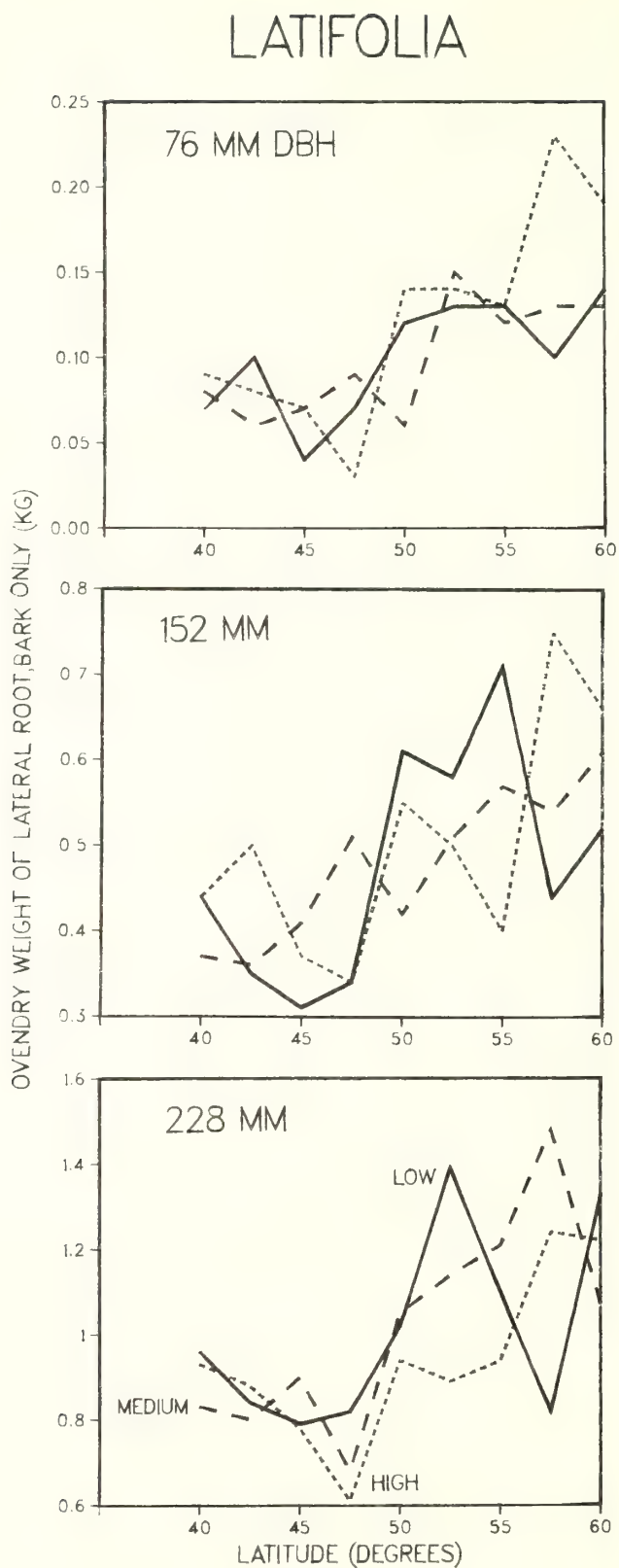


Figure 4-95—Ovendry weight of bark of lateral roots from *latifolia* trees of three diameters, related to latitude and elevational zone.

Central Root Mass-Taproot, Wood Plus Bark

Specific Gravity—Specific gravity of the central root mass-taproot is second only to the stump (table 4-2), averaging 0.468, with standard deviation of 0.052, based on oven-dry weight and green volume. In 76-mm trees, specific gravity of wood plus bark of the central root mass-taproot is positively correlated with latitude, but in larger trees there is little latitudinal trend (fig. 4-96); neither is there a strong trend related to elevational zone.

Trees 76, 152, and 228 mm in d.b.h. averaged 0.462 (0.050), 0.482 (0.057), and 0.460 (0.048).

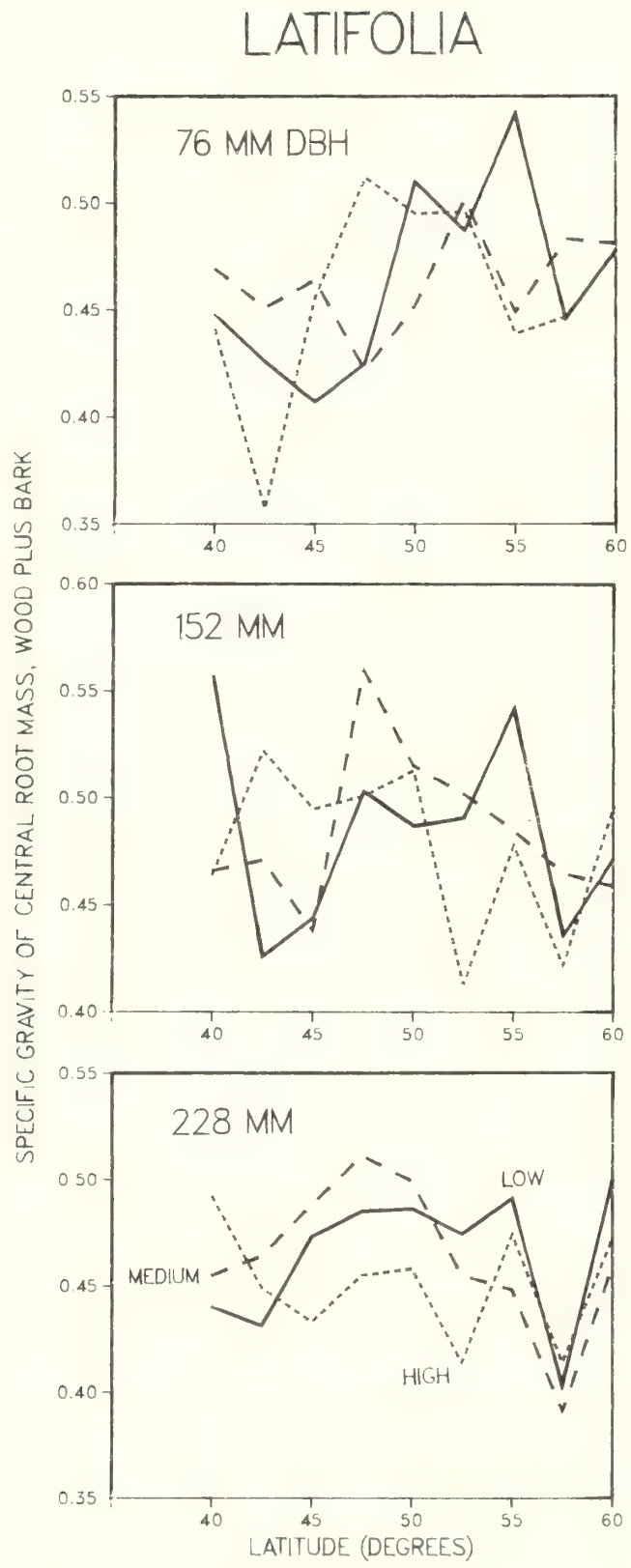


Figure 4-96—Specific gravity of wood plus bark from the central root mass-taproot (based on oven-dry weight and green volume) of *latifolia* trees of three diameters, related to latitude and elevational zone.

Weight, Green—In southern latitudes trees from low-elevation zones had heavier central root mass-taproots than those from high zones (fig. 4-97); on average, other latitudinal effects were minor.

Green weight of wood plus bark of this tree component was positively correlated with d.b.h., however, averaging 1.62 (0.53), 8.40 (2.51), and 20.46 (5.76) for trees 76, 152, and 228 mm in d.b.h.

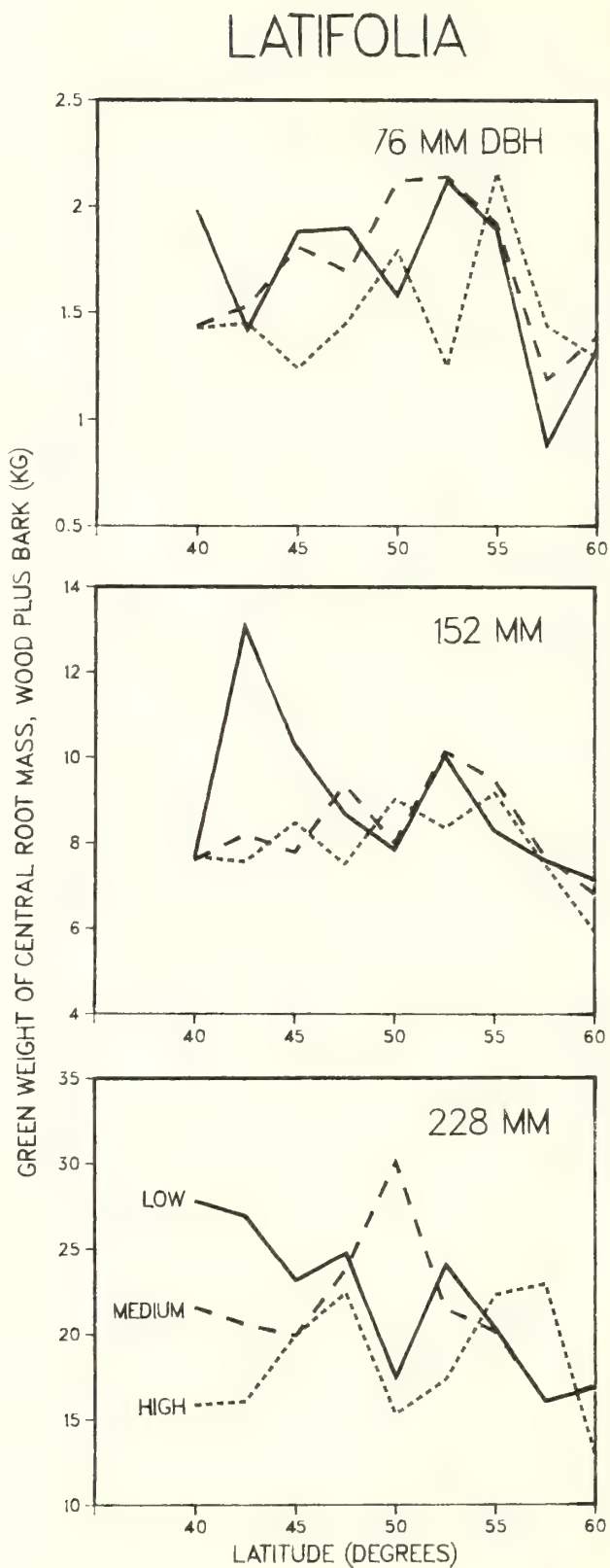


Figure 4-97—Green weight of wood plus bark of the central root mass-taproot of *latifolia* trees of three diameters, related to latitude and elevational zone.

LATIFOLIA

Weight, Ovendry—When ovendried, southern-latitude trees from low-elevation zones also had heavier central root mass-taproots than those from high zones (fig. 4-98). Average ovendry weights were highest (6.02 kg) at 47.5 degrees latitude and lowest (4.56 kg) at 60 degrees.

Ovendry weights, wood plus bark, were positively correlated with d.b.h., averaging 0.81 (0.27), 4.45 (1.28), and 10.74 (2.81) kg for trees of the three diameter classes.

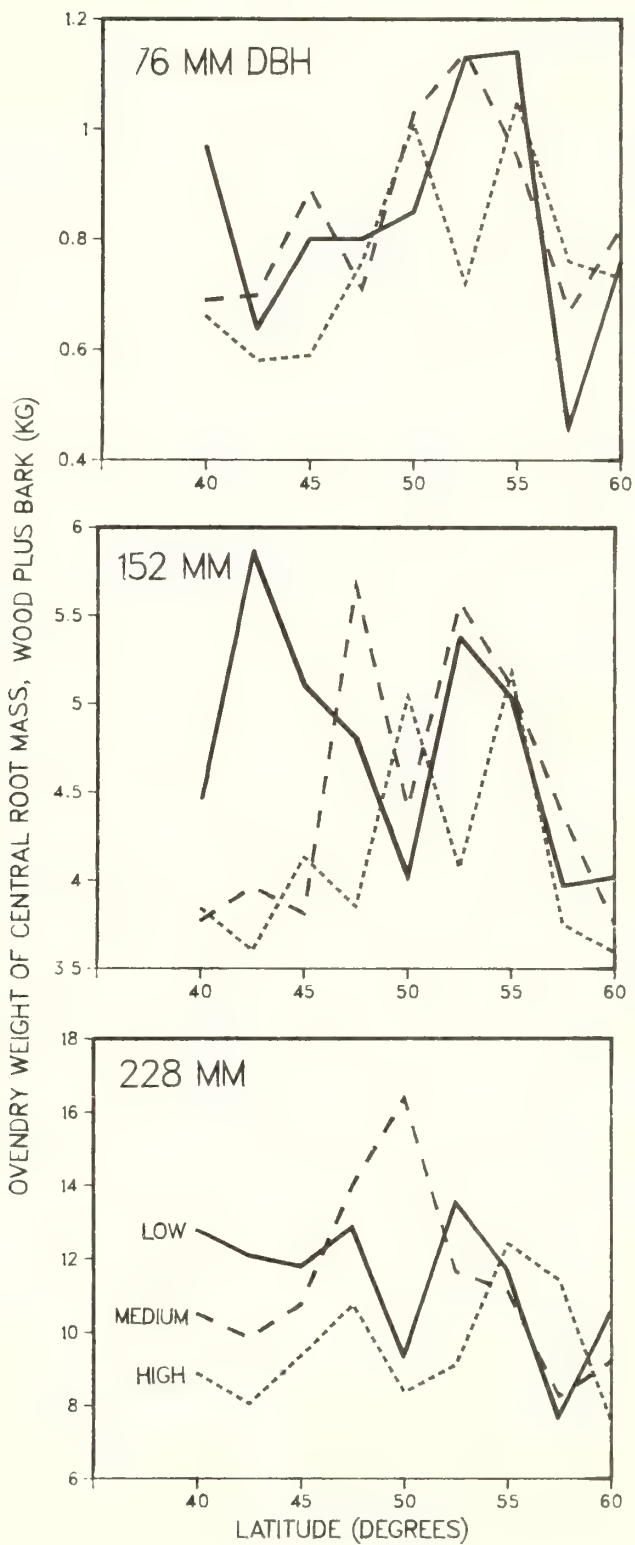


Figure 4-98—Ovendry weight of wood plus bark of the central root mass-taproot of *latifolia* trees of three diameters, related to latitude and elevational zone.

LATIFOLIA

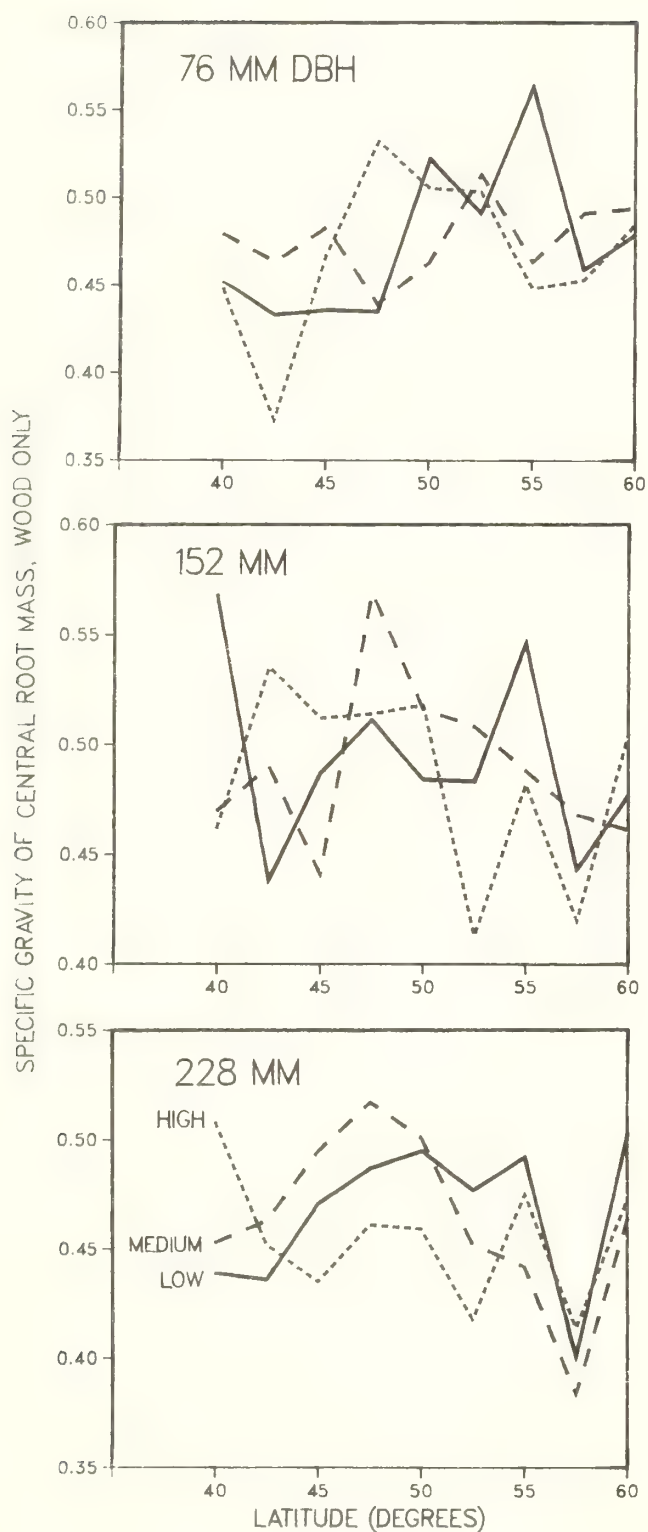


Figure 4-99—Specific gravity of wood of the central root mass-taproot (based on ovendry weight and green volume) from *latifolia* trees of three diameters, related to latitude and elevational zone.

Central Root Mass-Taproot, Wood Only

Specific Gravity—Specific gravity of the wood of the central root mass-taproot was second only to stumpwood, averaging 0.475, with standard deviation of 0.055, based on ovendry weight and green volume. Trees from low-elevation zones tended to have specific gravities in this root portion greater than those from high zones (0.478 vs. 0.469, with diameter data pooled). Except in 76-mm trees, where specific gravity was positively correlated with latitude, latitudinal trends were not pronounced—average values ranging from a minimum of 0.437 at 57.5 degrees to a maximum of 0.496 at 50 degrees (fig. 4-99).

Specific gravity of wood of this root portion in trees 76, 152, and 228 mm in d.b.h. averaged 0.473 (0.052), 0.489 (0.060), and 0.462 (0.051).

Weight, Green—In most latitudes south of 55 degrees, trees from low-elevation zones had more weight of green wood in the central root mass-taproot than those from high zones (fig. 4-100). Green weights averaged least at the two extremes of latitude—40 and 60 degrees.

Weights of green wood from this root portion were positively correlated with d.b.h., averaging 1.40 (0.46), 7.54 (2.22), and 18.72 (5.24) kg for trees 76, 152, and 228 mm in d.b.h.

Weight, Ovendry—Weights of ovendry wood of this root portion averaged maximum at middle latitudes and minimum in the two southern and two northern latitudes (fig. 4-101). As with green wood of this root portion, south of 55 degrees latitude most trees from low-elevation zones had more weight of ovendry wood in the central root mass-taproot than trees from high zones.

Weight of ovendry wood from this root portion was positively correlated with d.b.h., averaging 0.71 (0.24), 4.02 (1.15), and 9.86 (2.56) kg for trees of the three diameter classes.

LATIFOLIA

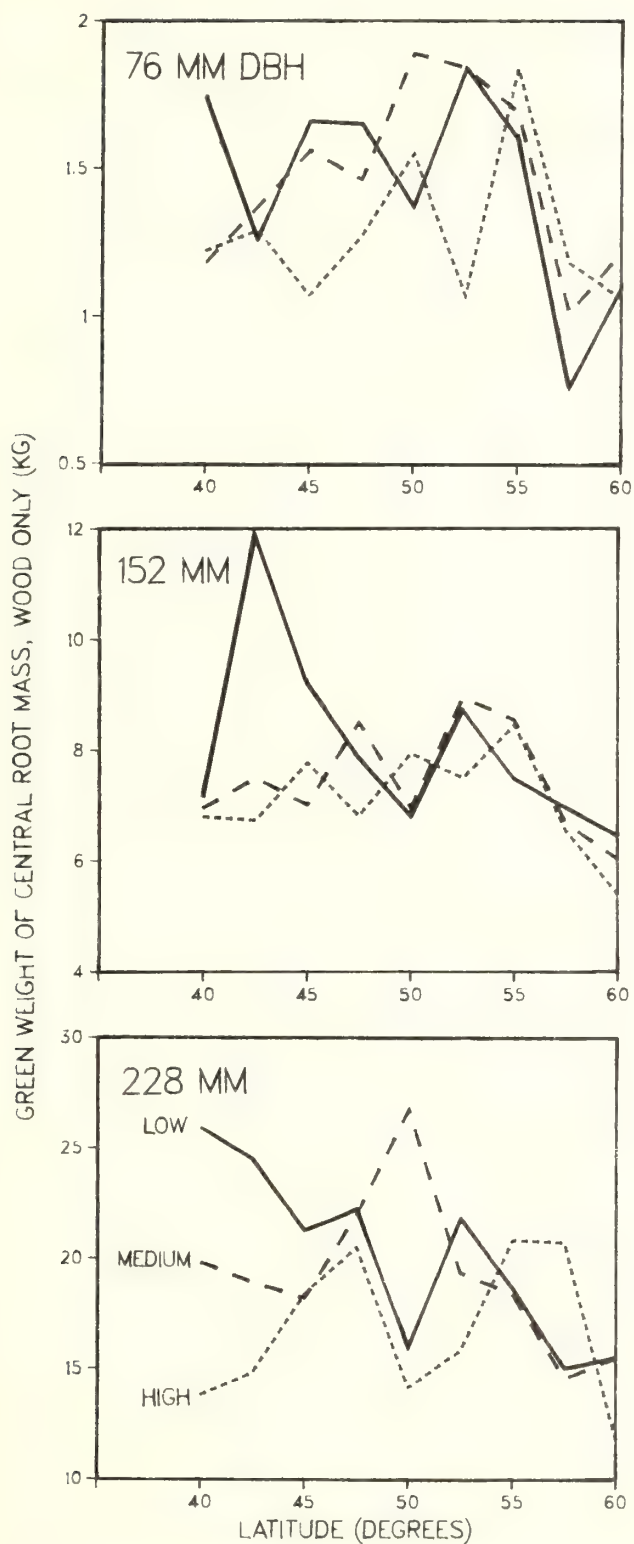


Figure 4-100—Green weight of wood from the central root mass-taproot of *latifolia* trees of three diameters, related to latitude and elevational zone.

LATIFOLIA

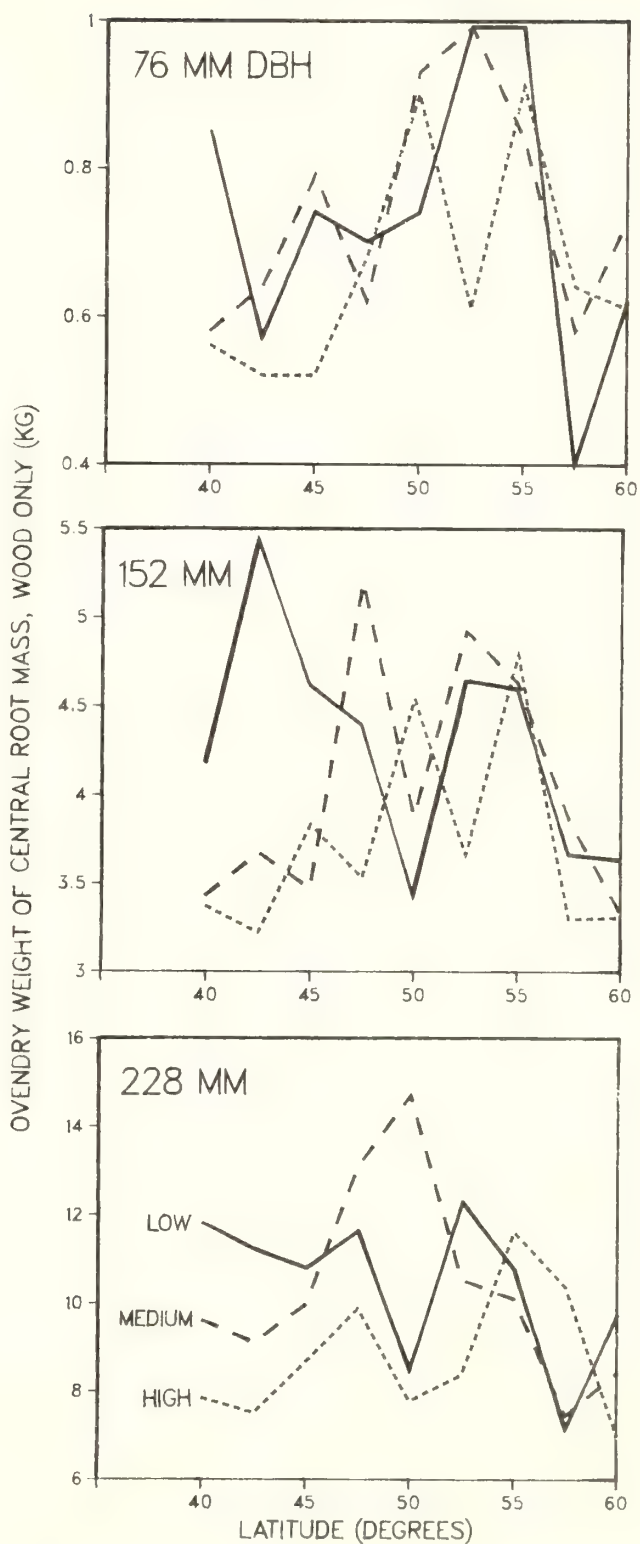


Figure 4-101—Oven-dry weight of wood from the central root mass-taproot of *latifolia* of three diameters, related to latitude and elevational zone.

LATIFOLIA

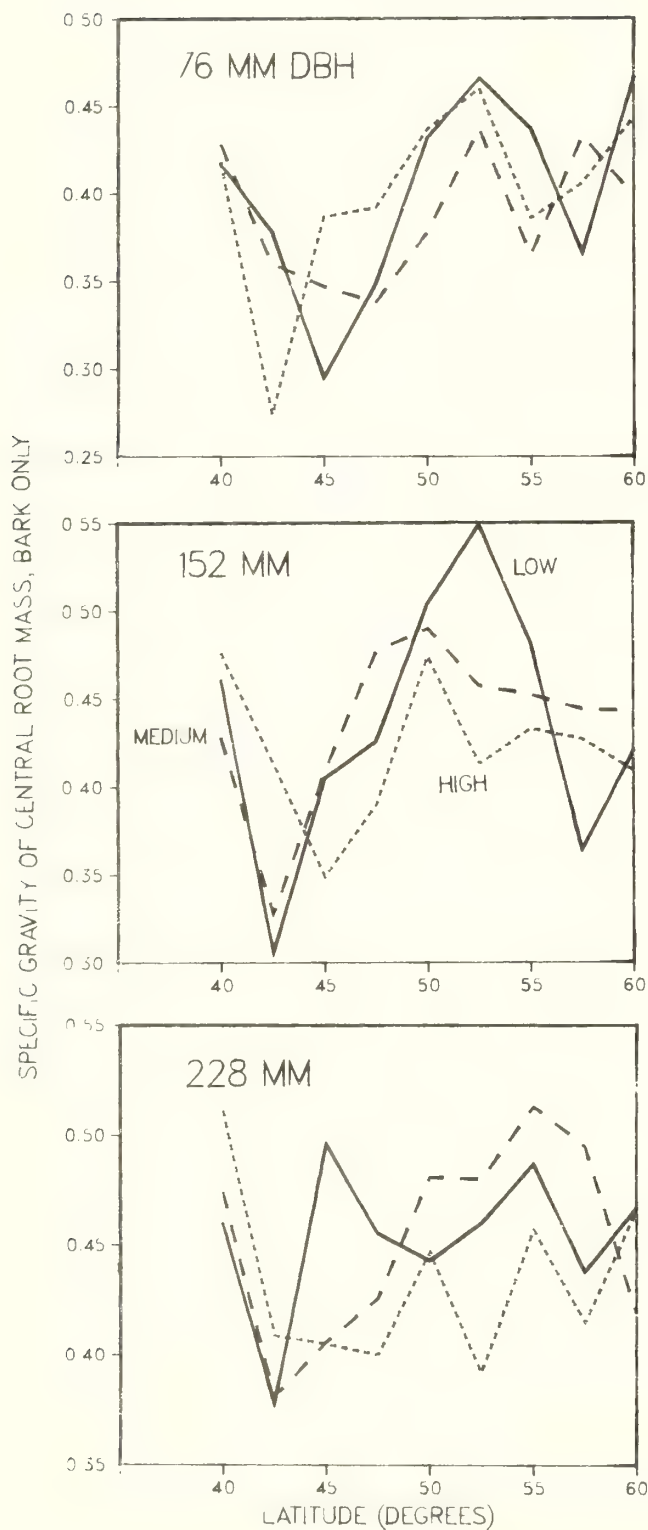


Figure 4-102—Specific gravity of bark (based on oven-dry weight and green volume) from the central root mass-taproot of *latifolia* trees of three diameters, related to latitude and elevational zone.

Central Root Mass-Taproot, Bark Only

Specific Gravity—Specific gravity of the bark of the central root mass-taproot was second only to that of stumppark (table 4-2), averaging 0.425, with standard deviation of 0.066. At most latitudes it was inversely correlated with elevational zone, averaging 0.430, 0.425, and 0.418 in low, medium, and high zones. It averaged minimum (0.359 to 0.406) from 42.5 to 47.5 degrees latitude; in other latitudes it exceeded 0.420 (fig. 4-102).

Specific gravity of bark of this root portion was positively correlated with d.b.h., averaging 0.396 (0.064), 0.431 (0.065), and 0.447 (0.060) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—In most latitudes weight of green bark of the central root mass-taproot was greater in low-elevation zones than in high (fig. 4-103). It averaged least (0.72 to 0.90 kg) in the three northernmost latitudes and maximum (1.02 to 1.08 kg) in the three middle latitudes.

Weights of green bark from this root portion were positively correlated with d.b.h., averaging 0.23 (0.09), 0.87 (0.39), and 1.75 (0.68) kg for trees of the three diameter classes.

Weight, Oven-dry—Also when oven-dry, weight of bark from the central root mass-taproot was usually greater in low-elevation zones than in high (fig. 4-104). It averaged least (0.38 and 0.39 kg) at 42.5 and 60 degrees latitude and most (0.56 and 0.59 kg) at 50 and 52.5 degrees.

Weights of oven-dry bark from this root portion were positively correlated with d.b.h., averaging 0.10 (0.04), 0.43 (0.19), and 0.88 (0.34) kg for trees 76, 152, and 228 mm in d.b.h.

LATIFOLIA

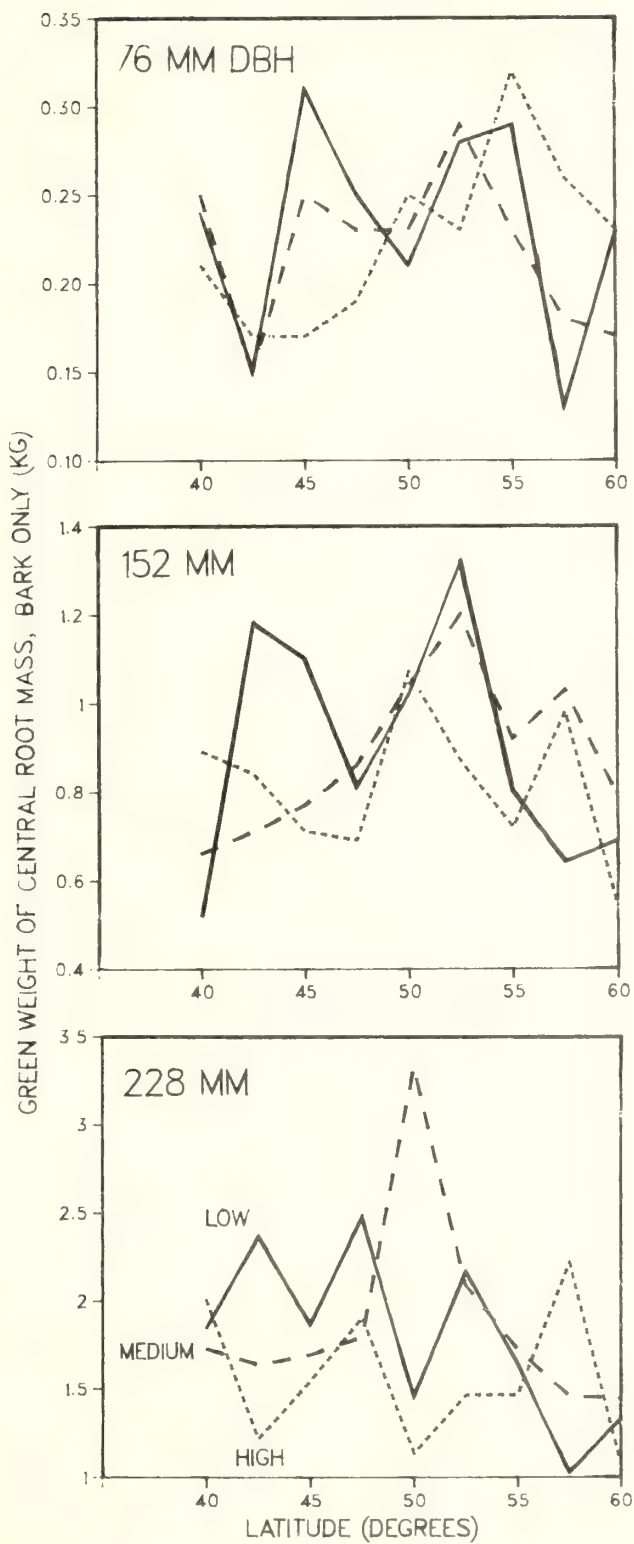


Figure 4-103—Green weight of bark from the central root mass-taproot of *latifolia* trees of three diameters, related to latitude and elevational zone.

LATIFOLIA

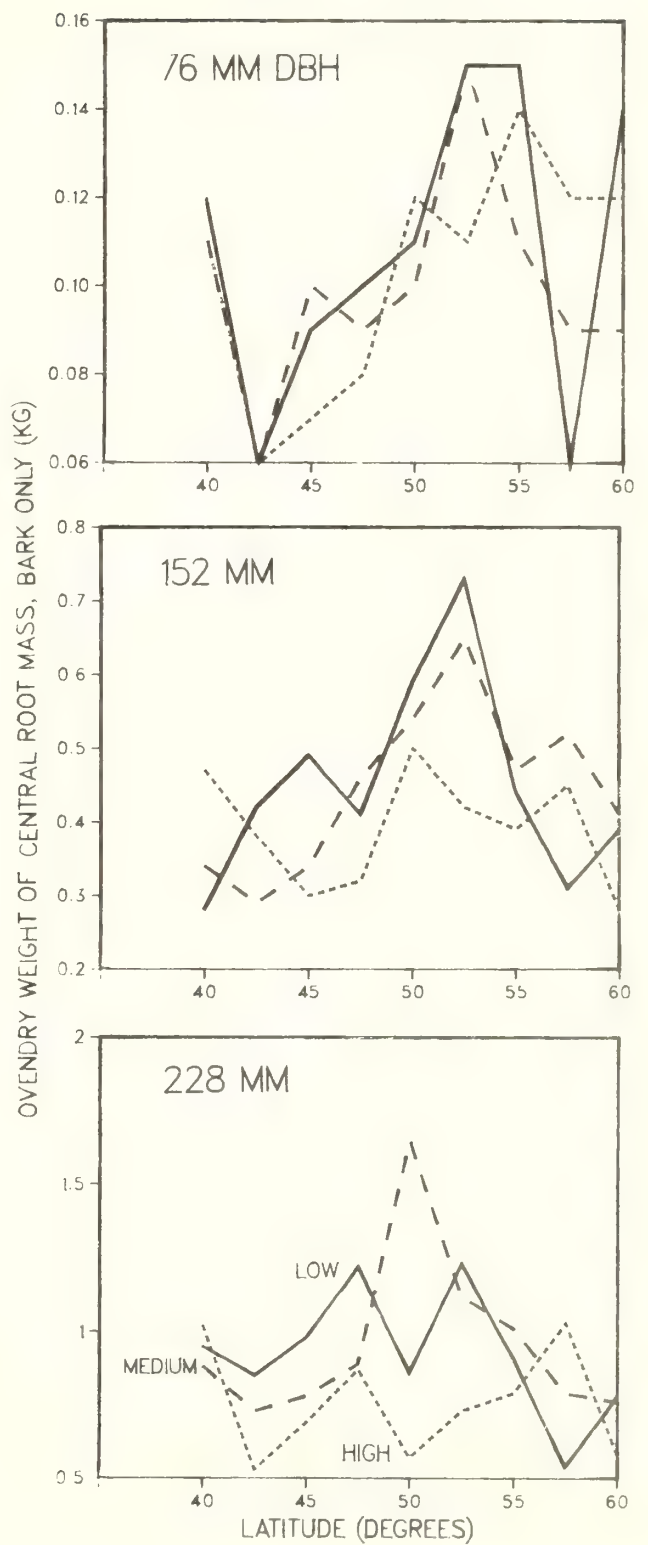


Figure 4-104—Oven-dry weight of bark from the central root mass-taproot of *latifolia* trees of three diameters, related to latitude and elevational zone.

4-6 RESULTS—MURRAYANA

For trees of variety *murrayana*, the three d.b.h. classes averaged 76 mm with standard deviation of 1.8 mm, 151 mm with standard deviation of 2.9 mm, and 229 mm with standard deviation of 3.9 mm. All were selected at medium elevation, which for the four latitudes averaged as follows (fig. 1-1):

Latitude	Elevation	General location
Degrees	Meters	
37.5	2,402	Just east of Yosemite National Park
40	1,676	Vicinity of Quincy, CA
42.5	2,006	Southwest of Paisley, OR
45	1,148	North of Breitenbush, OR

Because the entire *murrayana* sample totaled but 36 trees, correlations among tree characteristics are not noted in the detail provided for the 243 *latifolia* trees. It is worth noting, however, that for the 36 *murrayana* trees, stemwood specific gravity and average growth-ring width at 152-mm stump height were more closely correlated than in *latifolia* trees. The *murrayana* equation follows ($R^2 = 0.312$; standard error of the estimate = 0.0449):

$$G = 0.5462 - 0.0519W$$

where:

G = stemwood specific gravity at 152-mm stump height, basis of ovendry weight and green volume

W = average growth-ring width at 152-mm stump height, mm.

This equation is applicable only at 152-mm stump height, where stemwood specific gravity averaged 0.488 and growth-ring width averaged 1.12 mm.

Standard deviations for diameter-class data are noted in parentheses following their average values, as they were in the *latifolia* results section.

Even with this small sample (nine trees per latitude), numerous latitudinal differences were observed. Only those statistically significant (0.05 level) are graphed or tabulated.

Average specific gravities of tree components are summarized in table 4-2, weights in table 4-3, major tree component proportions of weight in table 4-4, bark weight proportions of components in table 4-5, and green weights of the three major tree components required to yield 1 m³ of wood in table 4-6; interpretation of these averages requires reference to the main effects and interaction attributable to d.b.h., latitude, and elevational zone—as discussed in the following paragraphs.

Complete Tree With Cones and Foliage

Weight, Green—Complete-tree green weight was not significantly related to latitude, but was positively correlated with tree d.b.h., averaging 24.25 (4.48), 151.57 (34.30), and 419.37 (76.70) kg for the three diameter classes.

Weight, Ovendry—Similarly, complete-tree ovendry weight was unrelated to latitude, but was positively correlated with d.b.h., averaging 12.11 (2.43), 72.95 (19.03), and 197.65 (43.03) kg for the three diameter classes.

Complete Tree Without Cones or Foliage

Specific Gravity—Complete-tree specific gravity (wood plus bark—but not foliage—of all components) significantly increased from south to north (fig. 4-105, top), and was negatively correlated with d.b.h., averaging 0.464 (0.033), 0.438 (0.036), and 0.413 (0.025) for 76-, 152-, and 228-mm trees, respectively (fig. 4-105, top).

Weight, Green—Without foliage, complete-tree green weight was unrelated to latitude, but was positively correlated with d.b.h., averaging 22.45 (4.35), 143.38 (34.83), and 399.54 (78.32) kg for the three diameter classes.

Weight, Ovendry—Similarly, foliage-free complete-tree ovendry weight was unrelated to latitude, but averaged 11.28 (2.44), 69.02 (19.43), and 188.37 (44.07) kg for the three diameter classes.

Complete Tree, Wood Only

Specific Gravity—Treewood specific gravity (data from stem, branches, and stump-root system included) generally increased from south to north in the two larger diameter classes (fig. 4-105, center), and was negatively correlated with d.b.h., averaging 0.482 (0.039), 0.440 (0.042), and 0.407 (0.031) for trees 76, 152, and 228 mm in d.b.h., respectively.

Weight, Green—Treewood green weight was not significantly related to latitude, but was positively correlated with d.b.h., averaging 19.02 (3.88), 127.59 (33.27), and 362.34 (77.26) kg for the three diameter classes.

Weight, Ovendry—Correspondingly, ovendry weight of complete-tree wood averaged 9.74 (2.26), 61.44 (18.66), and 169.91 (43.38) kg for the three diameter classes.

Complete Tree, Bark Only

Specific Gravity—Specific gravity of treebark (data from stem, branches, and stump-root system included) did not vary with tree d.b.h., and averaged 0.379, with standard deviation of 0.033. It did, however, vary with latitude, with maximum of 0.404 at 42.5 degrees and minimum of 0.355 at 37.5 degrees (fig. 4-105, bottom).

Weight, Green—Green bark weight of the complete tree was unrelated to latitude, but was positively correlated with d.b.h., averaging 3.39 (0.69), 15.54 (2.51), and 36.37 (5.51) kg for the three diameter classes, respectively.

Weight, Ovendry—Correspondingly, ovendry weight of complete-tree bark averaged 1.51 (0.29), 7.36 (1.05), and 17.77 (2.91) kg for the three diameter classes.

MURRAYANA

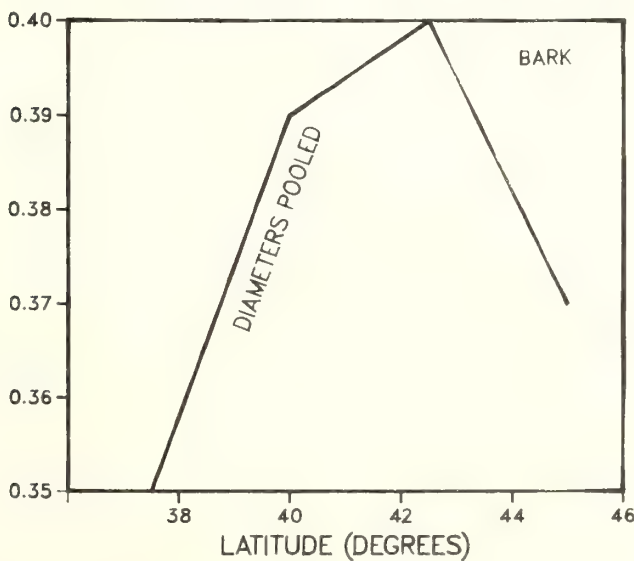
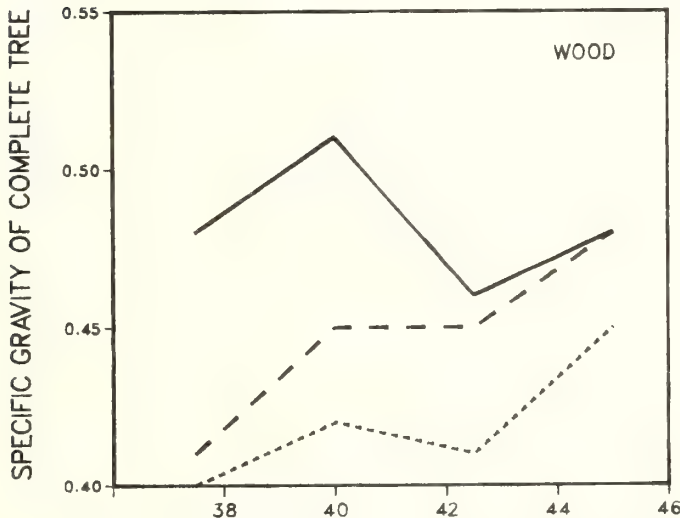
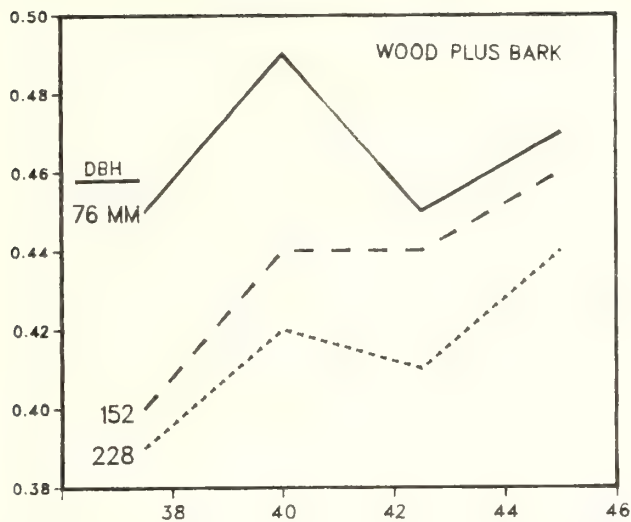


Figure 4-105—Specific gravity (based on oven-dry weight and green volume) of wood plus bark, wood only, and bark only of complete *murrayana* trees of three diameters, related to latitude.

Percentage of Weight of Gross Foliage-Free Complete Tree, Green and Oven-dry—Treebark percentage of gross foliage-free complete-tree weight was inversely correlated with latitude (fig. 4-106) and with d.b.h., as follows:

D.b.h. mm	Moisture condition	
	Green	Oven-dry
76	15.25 (2.55)	13.67 (2.26)
152	11.31 (2.41)	11.31 (2.54)
228	9.45 (2.58)	9.56 (3.12)

MURRAYANA

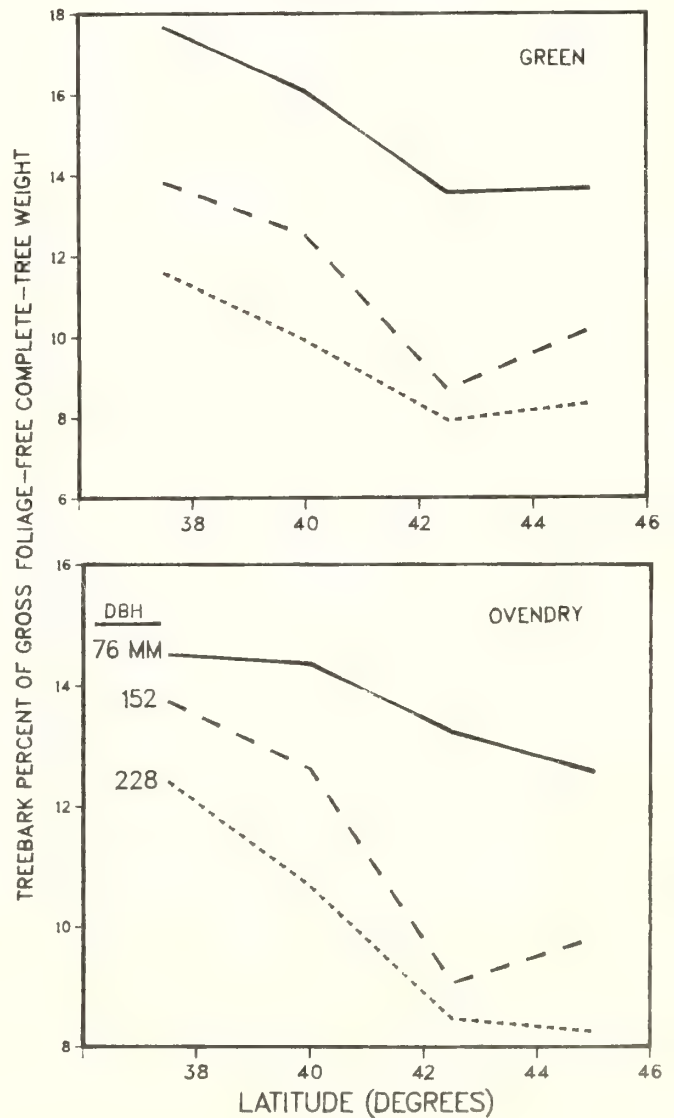


Figure 4-106—Treebark (from branches, stem, and stump-root system) as percentage of gross foliage-free complete-tree weight—green and oven-dry, for *murrayana* trees of three diameters, related to latitude.

Foliage

Weight, Green—Technical-foliage green weight per tree was unrelated to latitude, but was positively correlated with d.b.h., averaging 1.81 (0.81), 8.19 (3.52), and 19.83 (5.39) kg for the three diameter classes.

Weight, Ovendry—Correspondingly, ovendry foliage weight averaged 0.83 (0.38), 3.94 (1.79), and 9.28 (2.50) for the three diameter classes.

Tree Component Proportion, Green-Weight Basis—On a green-weight basis foliage as a percentage of complete-tree weight was unrelated to either latitude or d.b.h., with overall average of 6.12 percent and standard deviation of 3.19 percentage points.

Tree Component Proportion, Ovendry-Weight Basis—On an ovendry-weight basis, however, foliage as a percentage of complete tree weight was negatively correlated with latitude (fig. 4-107); average foliage weights were highest at 37.5 degrees (8.44 percent) and lowest at 45 degrees (4.09 percent). Overall dry-weight foliage proportion averaged 6.05 percent, with standard deviation of 3.43 percentage points.

MURRAYANA

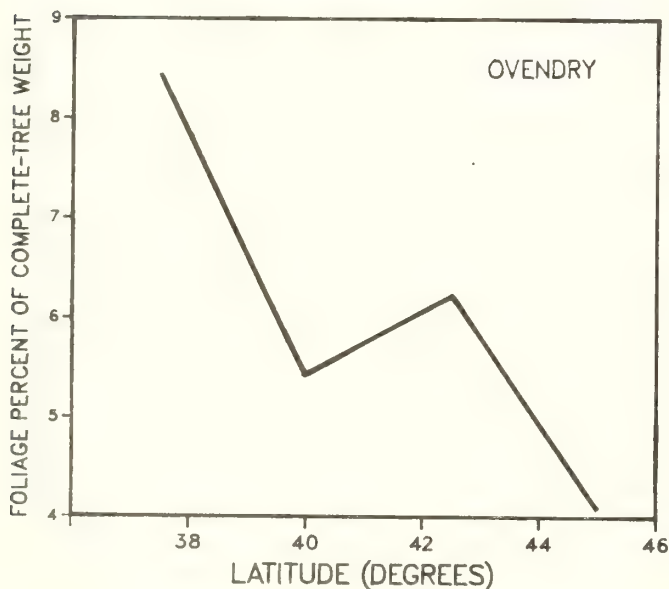


Figure 4-107—Foliage as percentage of complete-tree weight (ovendry basis) for *murrayana* trees, related to latitude; diameter data pooled.

Cones, Individual

Weight, Green—Individual green cone weight, as sampled from the tip 305 mm of the top 25 branches, was unrelated to latitude or d.b.h., with overall average of 4.90 g per cone and standard deviation of 0.92 g.

Weight, Ovendry—Similarly, dry cone weight was unrelated to either latitude or d.b.h., and averaged 4.11 g, with standard deviation of 0.99 g.

All Cones on Tree

As explained in chapter 1, weight of all cones on each tree was computed, not measured directly, and therefore results should be interpreted with caution.

Weight, Green—Green weight of all cones on each tree was unrelated to latitude but was positively correlated with d.b.h., averaging 38 (105), 246 (221), and 833 (572) g for the three diameter classes.

Weight, Ovendry—Similarly, ovendry weight averaged 31 (86), 209 (190), and 691 (513) g for the three diameter classes.

Tree Component Proportion, Green-Weight Basis—Weight of green cones averaged 0.14 (0.36), 0.17 (0.17), and 0.21 (0.17) percentage of green complete-tree weight for trees 76, 152, and 228 mm in d.b.h.; these percentages were unrelated to latitude.

Tree Component Proportion, Ovendry-Weight Basis—Similarly, weight of ovendry cones averaged 0.22 (0.61), 0.30 (0.31), and 0.37 (0.32) percent of ovendry weight of complete trees of the three diameter classes.

Dead Branchwood

Weight, Green—Green weight of dead branches was greater in northern than in southern latitudes (fig. 4-108, top), and was positively correlated with d.b.h., averaging 0.26 (0.18), 1.08 (0.69), and 4.91 (4.50) kg for the three diameter classes.

Weight, Ovendry—Latitudinal trends were similar on an ovendry-weight basis (fig. 4-108, bottom); ovendry dead-branch weights per tree averaged 0.21 (0.15), 0.89 (0.57), and 4.34 (3.64) kg for the three diameter classes.

MURRAYANA

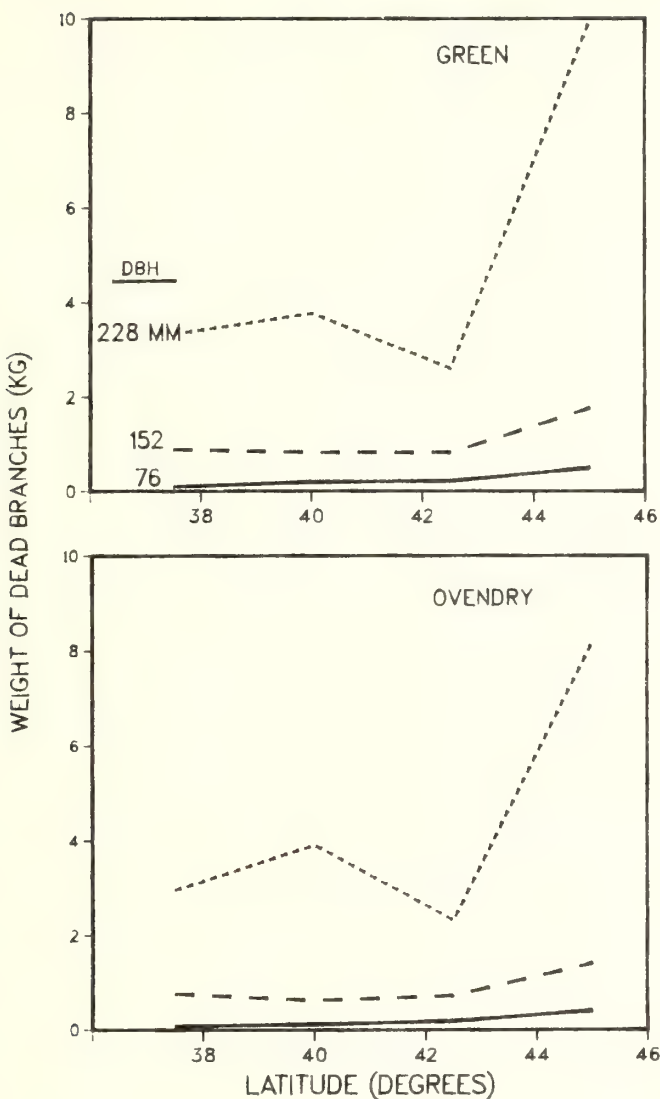


Figure 4-108—Weight of dead branches on *murrayana* trees of three diameters, related to latitude.

Tree Component Proportion, Green-Weight Basis—Dead branches, green-weight basis, totaled 1.02 percent of complete-tree weight, with standard deviation of 0.84 percent; this proportion did not vary significantly with d.b.h., but was significantly higher at 45 degrees latitude than in the three southerly latitudes (fig. 4-109, top).

Tree Component Proportion, Ovendry-Weight Basis—On an ovendry-weight basis, dead branches comprised 1.77 percent of complete-tree weight, with standard deviation of 1.39 percent. Trees in southern latitudes had a smaller proportion of dead-branch weight than those at the northernmost latitude (fig. 4-109, bottom).

MURRAYANA

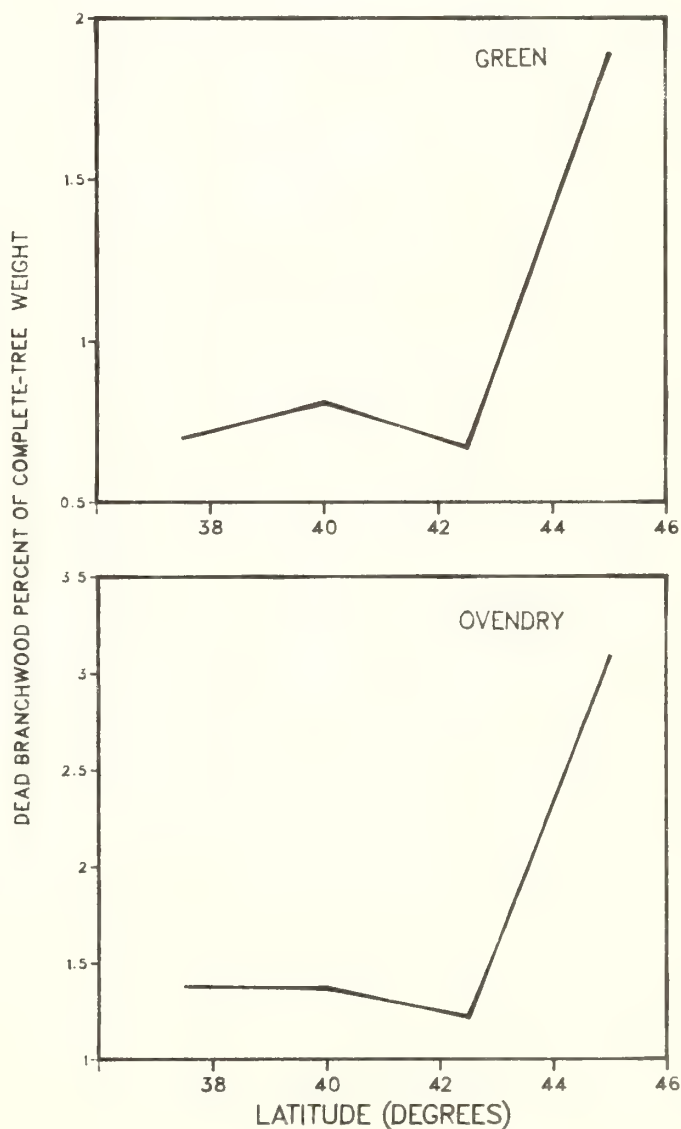


Figure 4-109—Dead branchwood as percentage of the weight of complete trees with foliage (green and ovendry) for *murrayana* trees related to latitude; diameter data pooled.

Live Branches, Wood Plus Bark

Specific Gravity—Specific gravity of live branches (wood plus bark) was unrelated to tree d.b.h., but varied with latitude (fig. 4-110, top); it was minimum (0.437) at 37.5 degrees and maximum at 42.5 degrees (0.477). Overall average was 0.458, with standard deviation of 0.024.

Weight, Green—The green weight of wood plus bark of foliage-free live branches was unrelated to latitude, but was positively correlated with d.b.h., averaging 1.25 (0.52), 7.85 (3.18), and 28.15 (13.05) kg for the three diameter classes.

Weight, Owendry—The owendry weight of wood plus bark of live branches was also unrelated to latitude and averaged 0.65 (0.26), 4.35 (1.60), and 13.82 (6.30) kg for the three diameter classes.

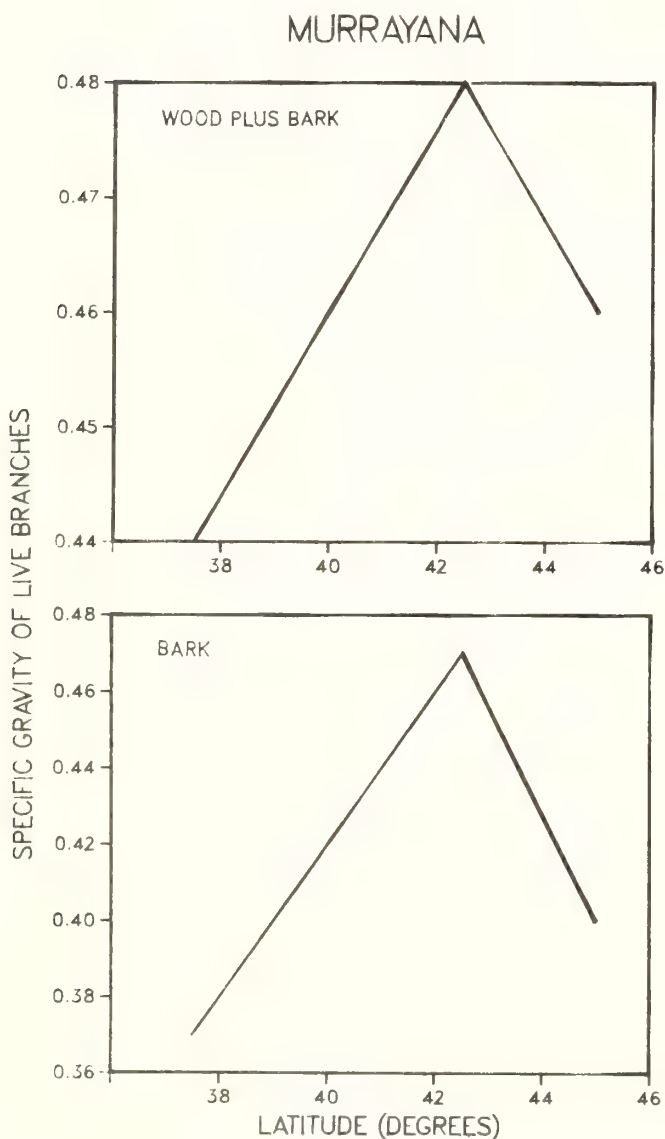


Figure 4-110—Specific gravity of live branches (wood plus bark and bark only) of *murrayana* trees, related to latitude; diameter data pooled.

Green Weight to Yield 1 m³ of Wood—Green weight of foliage-free branches required to yield 1 m³ of wood varied significantly with latitude (fig. 4-111); average requirement was highest at 40 degrees (1,735 kg) and lowest at 42.5 degrees (1,562 kg). It also was negatively correlated with d.b.h., averaging 1,854 (169), 1,584 (139), and 1,416 (147) kg for trees 76, 152, and 228 mm in d.b.h.

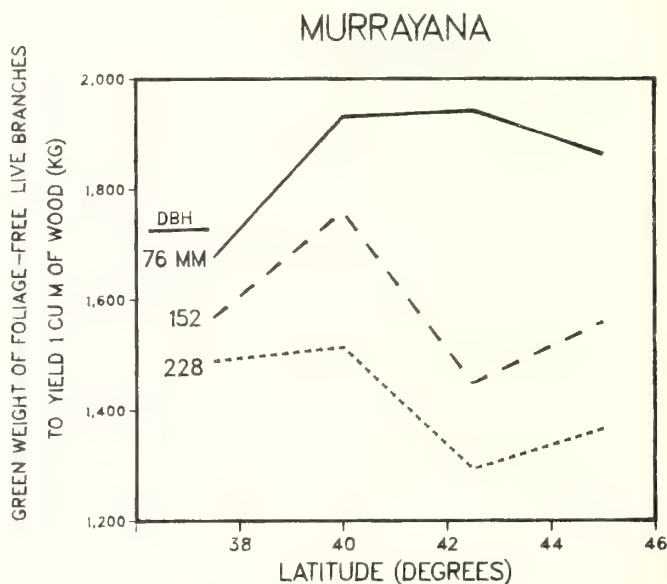


Figure 4-111—Green weight of live branches with bark (but after removal of technical foliage) required to yield 1 m³ of branchwood from *murrayana* trees of three diameters, related to latitude.

Tree Component Proportion, Green-Weight Basis—Live branch (wood plus bark) percentage of complete-tree green weight varied significantly with latitude (fig. 4-112, top); it was maximum at 37.5 degrees (8.95 percent) and minimum at 42.5 degrees (5.03 percent). The proportion was unrelated to d.b.h., with overall average of 6.04 percent and standard deviation of 3.59 percentage points.

Tree Component Proportion, Owendry-Weight Basis—On an owendry-weight basis the trend was similar (fig. 4-112, bottom), with maximum of 9.75 percent at 37.5 degrees and minimum of 4.22 percent at 42.5 degrees. The proportion was unrelated to d.b.h., with overall average of 6.71 percent and standard deviation of 4.08 percentage points.

Live Branchwood

Latitude was unrelated to specific gravity, or to green or oven-dry weights of branchwood.

Specific Gravity—Branchwood specific gravity was inversely correlated with tree d.b.h., averaging 0.509 (0.015), 0.495 (0.023), and 0.479 (0.018) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—Green branchwood weight was positively correlated with tree d.b.h., averaging 0.63 (0.28), 4.82 (1.88), and 18.58 (7.42) kg for the three diameter classes.

Weight, Oven-dry—Similarly, oven-dry branchwood weight averaged 0.35 (0.16), 2.69 (0.96), and 9.37 (3.68) kg for trees 76, 152, and 228 mm in d.b.h.

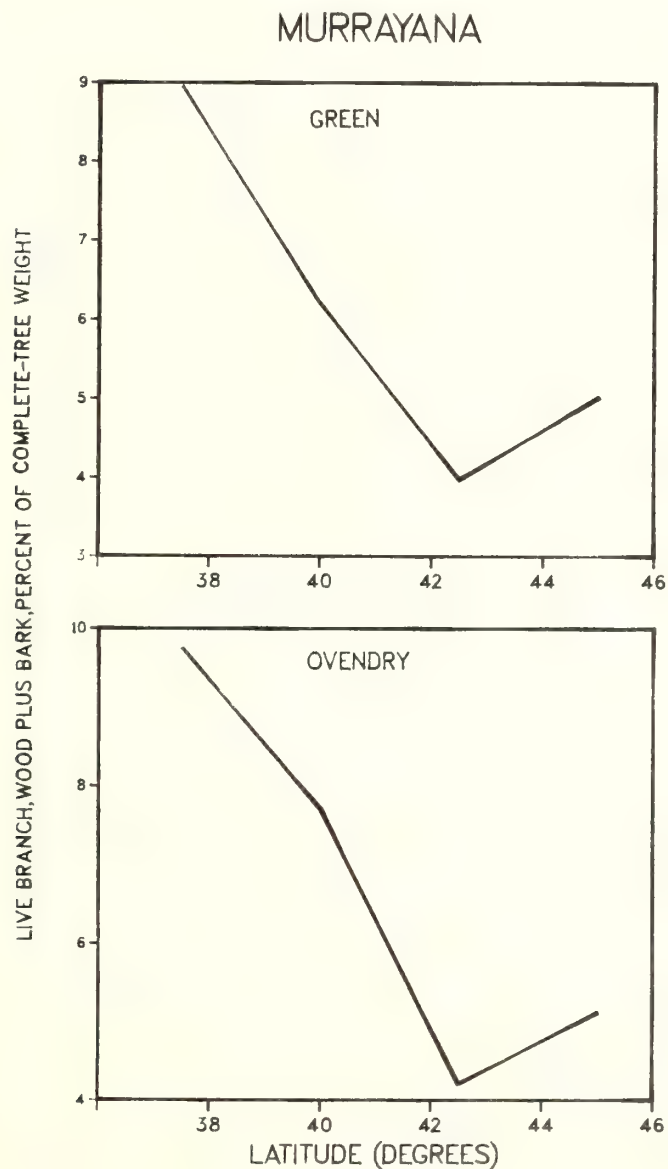


Figure 4-112—Live branches (wood plus bark) as percentage of the weight of complete *murrayana* trees with foliage—green and oven-dry—related to latitude; diameter data pooled.

Live Branchbark

Specific Gravity—Specific gravity of branchbark was unrelated to tree d.b.h., but was significantly related to latitude (fig. 4-110, bottom); it was minimum at 37.5 degrees (0.367) and maximum at 42.5 degrees (0.468).

Weight, Green—Green weight of branchbark was unrelated to latitude but was positively correlated with tree d.b.h., averaging 0.62 (0.26), 3.04 (1.40), and 9.56 (5.89) kg for trees of the three diameter classes.

Weight, Oven-dry—Similarly, oven-dry weight of branchbark averaged 0.31 (0.12), 1.65 (0.67), and 4.44 (2.77) kg for trees 76, 152, and 228 mm in d.b.h.

Live Branchbark as Percentage of Gross Live Branch

Weight, Green and Oven-dry—On a green-weight basis, bark of live branches averaged 40.05 percent of total foliage-free weight, but this proportion varied significantly with latitude (fig. 4-113) and with d.b.h., averaging 49.55 (5.12), 38.42 (4.78), and 32.20 (6.39) for trees 76, 152, and 228 mm in d.b.h.

On an oven-dry basis, only d.b.h. was significant; the bark proportions averaged 47.44 (6.46), 37.82 (3.19), and 30.67 (5.78) percent for trees 76, 152, and 228 mm in d.b.h.

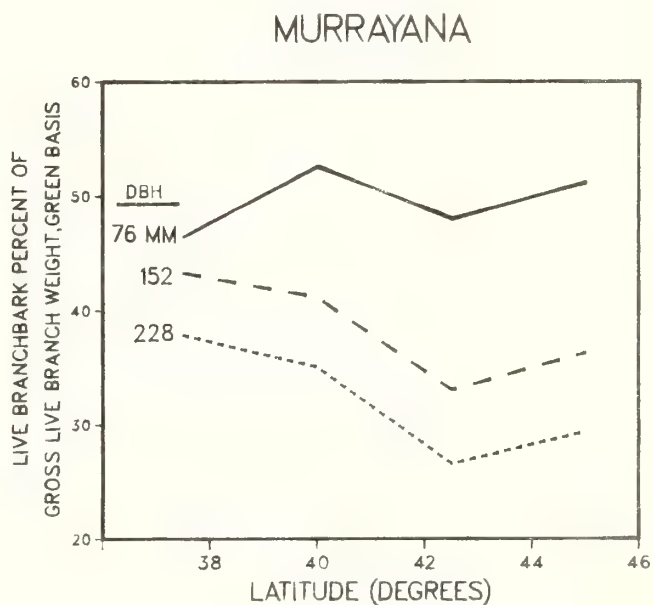


Figure 4-113—Live branchbark as percentage of gross live branch weight for *murrayana* trees of three diameters, related to latitude; green-weight basis.

Stem, Wood Plus Bark—Tree Average

Specific Gravity—Stem specific gravity (wood plus bark, from 152-mm stump height to apical tip) in smaller trees was positively correlated with latitude (fig. 4-114, top); it was negatively correlated with diameter, averaging 0.463 (0.035), 0.431 (0.038), and 0.404 (0.028) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—Wood plus bark of green stems was unrelated to latitude, but was positively correlated with d.b.h., averaging 17.16 (4.07), 113.41 (34.63), and 321.69 (83.64) kg for trees of the three diameter classes.

Weight, Ovendry—Similarly, ovendry weights averaged 8.59 (2.25), 54.17 (19.11), and 149.05 (45.76) kg for trees of the three diameter classes.

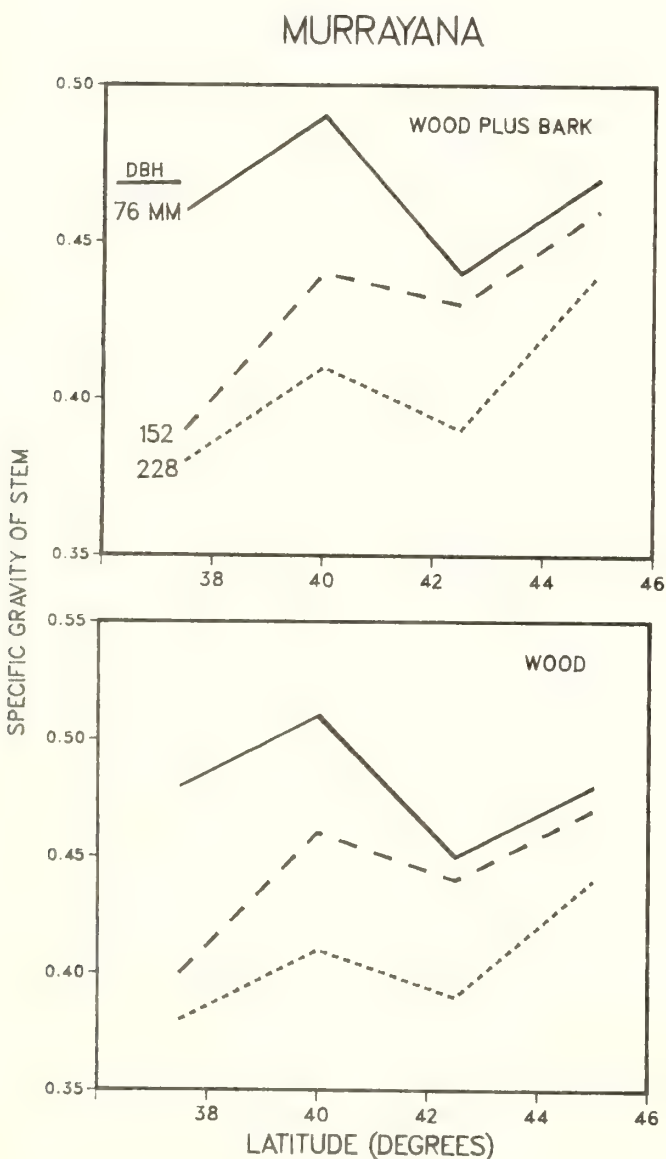


Figure 4-114—Average specific gravity (based on ovendry weight and green volume) for stems (wood plus bark and wood only) of *murrayana* trees of three diameters, related to latitude.

Green Weight to Yield 1 m³ of Wood—Green weight of stems with bark required to yield 1 m³ of wood was least at 42.5 degrees latitude for all three tree diameters (fig. 4-115). Although varying with latitude, the statistic was generally negatively correlated with d.b.h., averaging 1,093 (74), 1,030 (76), and 968 (67) kg for trees 76, 152, and 228 mm in d.b.h.

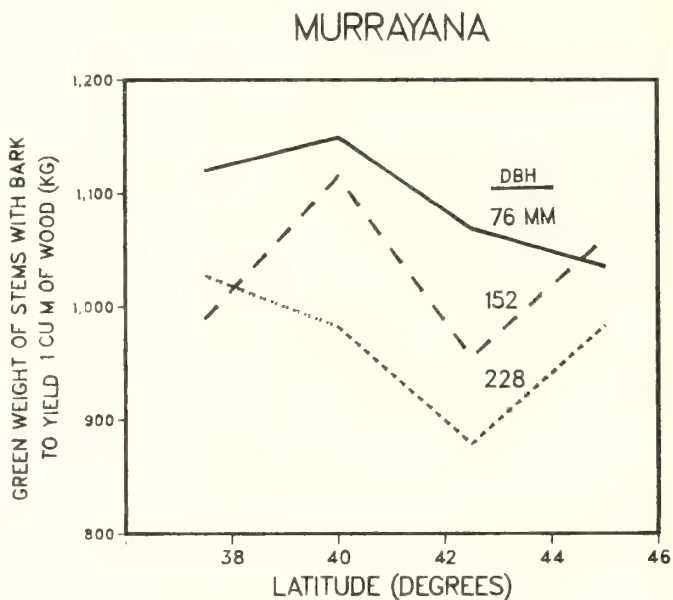


Figure 4-115—Green weight of stems with bark required to yield 1 m³ of stemwood from *murrayana* trees of three diameters, related to latitude.

Tree Component Proportion, Green-Weight Basis—The stems with bark averaged 73.1 percent of the green weight of complete trees with foliage; standard deviation was 8.6 percent. This percentage was not significantly related to d.b.h., but did vary significantly with latitude. It was least at 37.5 degrees (66.7 percent) and most at 45 degrees (fig. 4-116, top).

Tree Component Proportion, Ovendry-Weight Basis—On an ovendry-weight basis the overall average was 72.2 percent, with standard deviation of 8.8 percentage points. The percentage was least at 37.5 degrees latitude (65.4 percent) and most at 45 degrees (76.9 percent); see figure 4-116, bottom.

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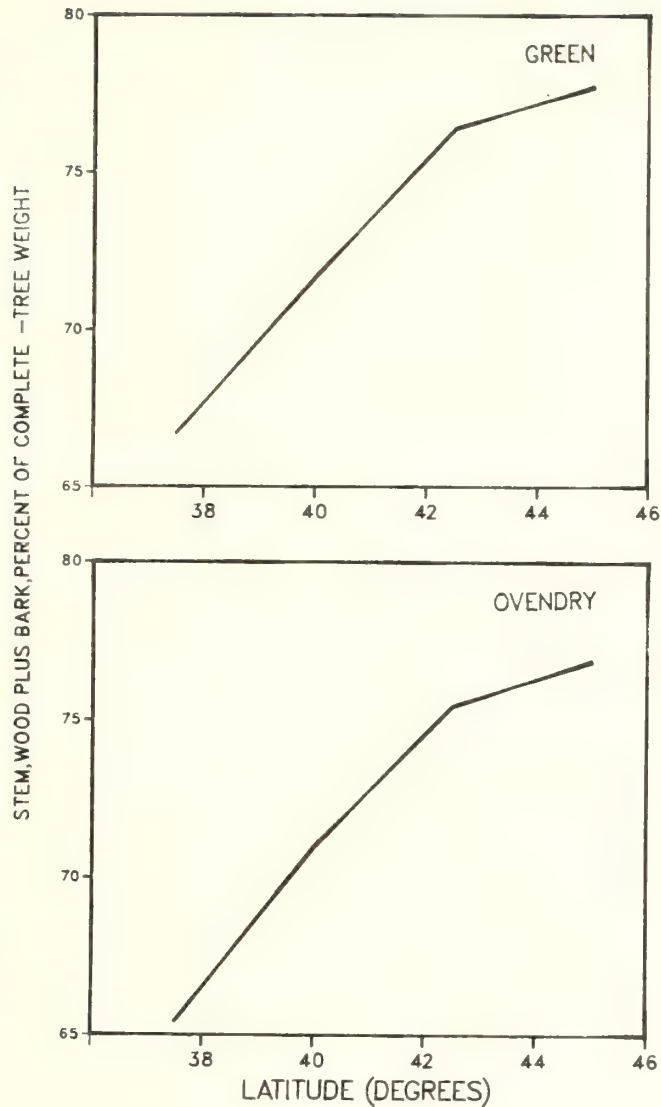


Figure 4-116—Stem (wood plus bark) as percentage by weight of complete *murrayana* trees with foliage—green and ovendry—related to latitude.

Stem, Wood Plus Bark—Variation With Height

Specific Gravity—The specific gravities of stems with bark diminish curvilinearly with height above stump (fig. 4-117). Curve forms are similar for the three d.b.h. classes studied, with small trees having consistently higher specific gravity than large trees at all levels below 90 percent of tree height. Specific gravity at 20 percent of tree height is near average for stems of these diameters (fig. 4-117).

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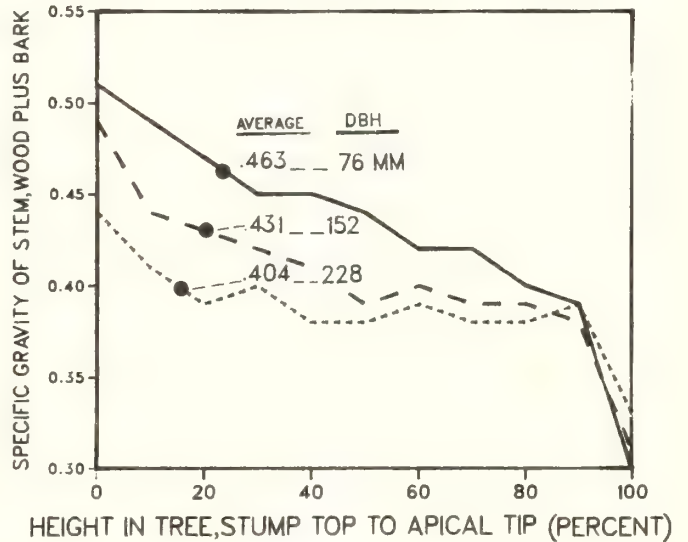


Figure 4-117—Stem, wood plus bark, specific gravity (based on ovendry weight and green volume) of *murrayana* trees of three diameters, related to height in tree. Stem average values are listed below each diameter designation.

Stemwood—Tree Average

Specific Gravity—Average entire stemwood specific gravity was inversely correlated with average growth-ring width at 152-mm stump height ($R^2 = -0.490$); that is, fast-grown trees had lower stemwood specific gravity than slow growers.

Average specific gravity of entire stemwood from 152-mm stump height to apical tip in *murrayana* trees of the diameters studied can be closely estimated from the specific gravity of a stemwood disk taken at 20 percent of tree height (figs. 4-118 and 4-119) by the following relationship ($R^2 = 0.937$; standard error of the estimate = 0.012):

Average stemwood specific gravity, ovendry weight and green volume basis =
 $0.0917 + 0.8014$ (stemwood specific gravity at 20 percent of tree height)

For trees 152 and 228 mm in d.b.h., average stemwood specific gravity was least at the southernmost latitude (fig. 4-114, bottom). Surprisingly, average stemwood specific gravity was inversely correlated with d.b.h., averaging 0.482 (0.039), 0.440 (0.042), and 0.407 (0.031) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—Stemwood weight, green basis—from 152-mm stump height to apical tip—was not significantly related to latitude, but was positively correlated with d.b.h., averaging 17.16 (4.07), 113.41 (34.63), and 321.69 (83.64) kg for the three diameter classes.

Weight, Ovendry—On an ovendry-weight basis, stemwood weight was only correlated with d.b.h., averaging 7.63 (2.09), 49.46 (18.04), and 137.55 (43.36) kg for the three diameter classes.

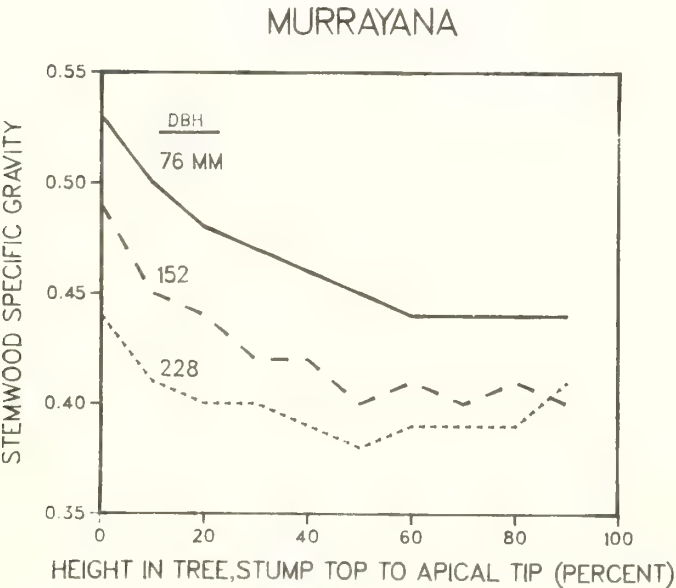


Figure 4-118—Stemwood specific gravity (based on ovendry weight and green volume) for *murrayana* trees of three diameters, related to height in tree.

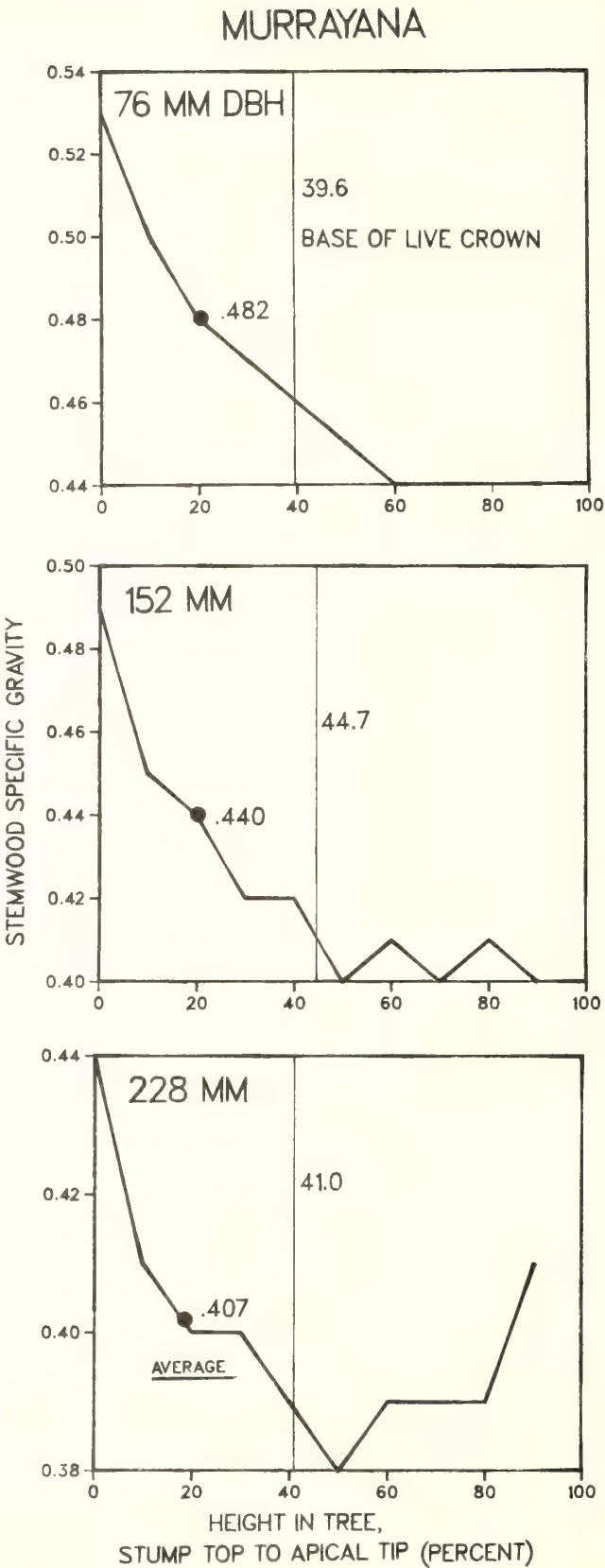


Figure 4-119—Stemwood specific gravity (based on ovendry weight and green volume) for *murrayana* trees of three diameters, related to height in tree, position of crown base, and position and value of stem average value of stemwood specific gravity.

Table 4-10—*Murrayana* stemwood specific gravities (basis of oven-dry weight and green volume) from 152-mm stump height to apical tip at 10 levels in trees of three breast-height diameters¹

Percent of stem height above stump	Diameter		
	76 mm	152 mm	228 mm
0	0.529 (0.051)	0.494 (0.037)	0.442 (0.030)
10	.504 (.041)	.448 (.042)	.441 (.042)
20	.480 (.048)	.440 (.052)	.395 (.042)
30	.466 (.044)	.424 (.050)	.401 (.039)
40	.462 (.043)	.416 (.053)	.386 (.035)
50	.455 (.031)	.403 (.048)	.384 (.031)
60	.443 (.029)	.407 (.041)	.393 (.029)
70	.444 (.025)	.399 (.043)	.387 (.037)
80	.439 (.030)	.409 (.039)	.387 (.024)
90	.440 (.034)	.404 (.033)	.408 (.036)

¹Latitudinal data pooled; standard deviations shown in parentheses following average values. Data based on 12 trees of each diameter.

Stemwood—Variation With Height

Specific Gravity—Stemwood specific gravity curvilinearly diminishes above stump height to near the base of the live crown, but then remains more or less constant within the live crown (table 4-10 and figs. 4-118 and 4-119). At all percentages of tree height below 90 percent, stemwood specific gravity is negatively correlated with tree d.b.h. (fig. 4-118). Stemwood specific gravity at 20 percent of tree height approximates stemwood-average specific gravity (fig. 4-119); see predictive equation under the preceding heading.

Stembark—Tree Average

Specific Gravity—Tree average stembark specific gravity was unrelated to either latitude or d.b.h.; it averaged 0.361, with standard deviation of 0.029.

Weight, Green—Green stembark weight was unrelated to latitude, but was positively correlated with d.b.h., averaging 2.18 (0.42), 10.00 (2.43), and 22.89 (4.65) kg for the three diameter classes.

Weight, Oven-dry—Similarly, stembark oven-dry weights for the three tree diameters averaged 8.59 (2.25), 54.17 (19.11), and 149.05 (45.76) kg.

Stembark as Percentage of Gross Stem Weight, Green and Oven-dry—Stembark percentage of the weight of stem with bark, green basis, averaged 9.77 percent, but averaged less in northern latitudes and more in southern latitudes (fig. 4-120). It also was negatively correlated with d.b.h., averaging 12.91 (1.83), 9.13 (1.49), and 7.26 (0.73) percent for trees 76, 152, and 228 mm in d.b.h.

On an oven-dry basis, stembark percentage by weight averaged 9.53 percent and was not significantly related to latitude (although averaging nearly two percentage points less in the two northern latitudes than in the two southern). It was negatively correlated with d.b.h., averaging 11.42 (1.75), 9.15 (1.56), and 8.01 (1.32) percent for the three diameter classes.

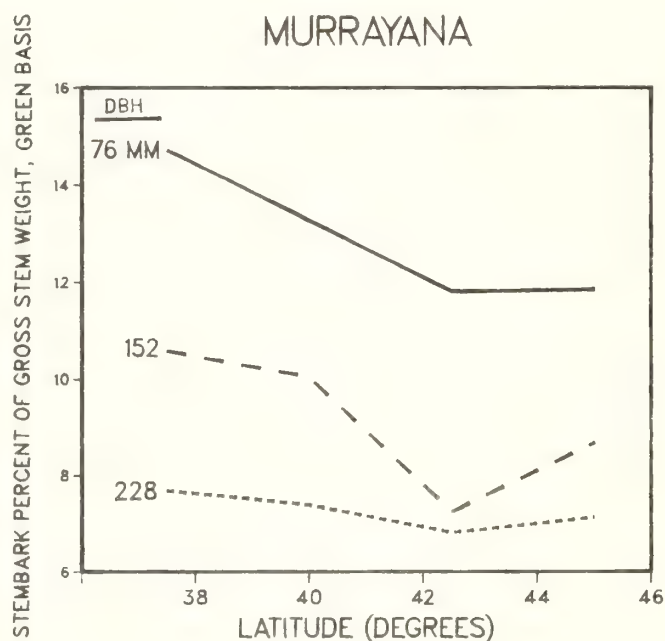


Figure 4-120—Stembark as percentage of gross stem weight in *murrayana* trees of three diameters, related to latitude.

Stembark—Variation With Height

Specific Gravity—Stembark specific gravity decreased curvilinearly with height in tree from a maximum at stump height of about 0.40 to a minimum of about 0.30 near the apical tip (fig. 4-121); shape and position of the curves did not vary significantly with tree d.b.h. Bark specific gravity at 20 percent of tree height approximates the tree average value (fig. 4-121).

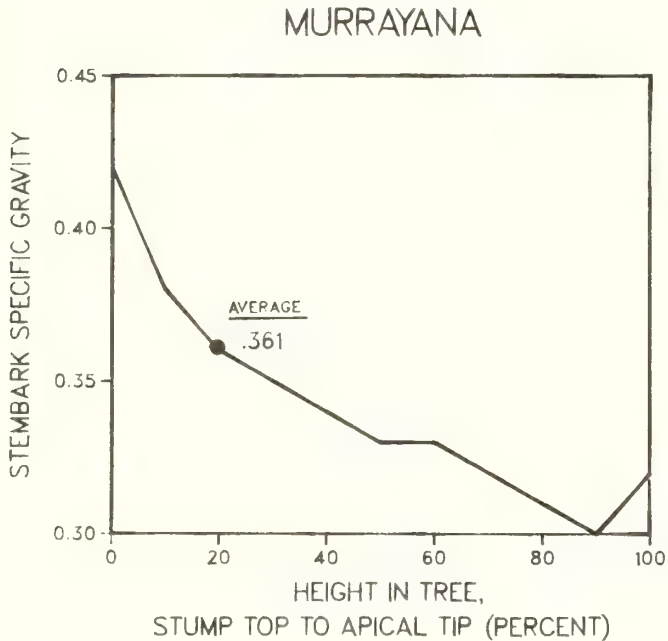


Figure 4-121—Stembark specific gravity (based on ovendry weight and green volume) of *murrayana* trees, related to height in trees; diameter data pooled.

Weight Percentage, Green—Stembark as a percentage of green stem weight is positively correlated with height in tree, varying from about 10 percent at stump height to over 20 percent at 90 percent of tree height, but is negatively correlated with tree d.b.h. (fig. 4-122, top); that is, small-diameter trees have a higher percentage of stembark at all heights in the stem than do large trees.

Weight Percentage, Ovendry—On an ovendry-weight basis (fig. 4-122, bottom), the weight-percentage relationship and values are similar to those on a green basis.

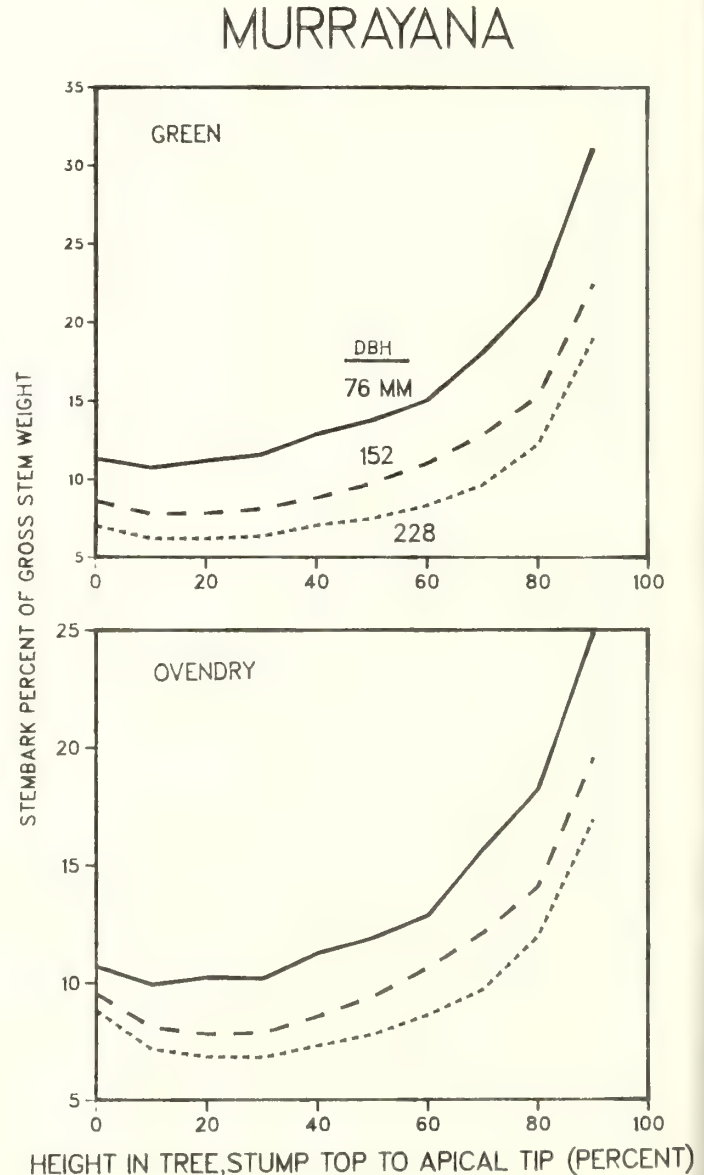


Figure 4-122—Stembark as percentage of gross stem weight, green and ovendry, in *murrayana* trees of three diameters, related to height in trees.

Sapwood

Specific Gravity—Sapwood specific gravity of the 152- and 228-mm trees averaged significantly less in the south than in the north (fig. 4-123, top). Also, sapwood specific gravity was negatively correlated with d.b.h., averaging 0.476 (0.038), 0.433 (0.044), and 0.401 (0.032) for trees 76, 152, and 228 mm in d.b.h. Overall average was 0.437, with standard deviation of 0.048.

Weight, Green—Sapwood weight, green basis, was not significantly related to latitude but was positively correlated with d.b.h., averaging 13.60 (3.48), 88.54 (25.48), and 253.53 (60.56) kg for trees of the three diameter classes.

Weight, Ovendry—Dry sapwood weight was also unrelated to latitude and positively correlated with d.b.h., averaging 6.74 (1.75), 39.00 (11.72), and 105.30 (26.76) kg for trees of the three diameter classes.

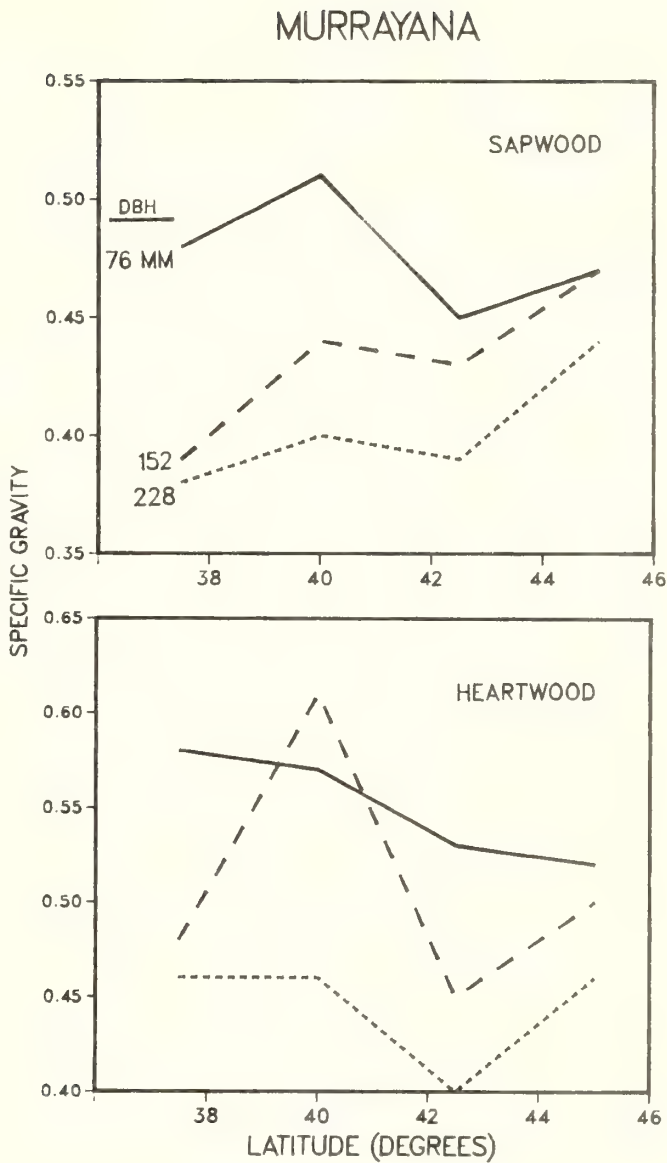


Figure 4-123—Average specific gravity (based on ovendry weight and green volume) of sapwood and heartwood of *murrayana* trees of three diameters, related to latitude.

Heartwood

Specific Gravity—Average heartwood specific gravity was highest (0.547) at 40 degrees and lowest (0.461) at 42.5 degrees (fig. 4-123, bottom). It was negatively correlated with d.b.h., averaging 0.550 (0.046), 0.508 (0.071), and 0.446 (0.037) for trees 76, 152, and 228 mm in d.b.h. Overall, heartwood specific gravity was greater than that of sapwood—probably because of a higher content of extractives, averaging 0.502, with standard deviation of 0.067. Information on the variation of heartwood and sapwood specific gravity with height in tree is given in figures 5-49 and 5-50 (see next chapter).

Weight, Green—Although heartwood specific gravity averaged least at 42.5 degrees latitude, green weight of heartwood was greatest at this latitude (fig. 4-124, top). Heartwood green weight was positively correlated with d.b.h. at all latitudes, averaging 1.38 (1.42), 14.88 (12.87), and 45.28 (29.60) kg for trees of the three diameter classes.

Weight, Ovendry—On an ovendry basis, latitudinal and diameter trends were similar (fig. 4-124, bottom), with heartwood weights for trees of the three diameter classes averaging 0.96 (0.99), 10.46 (9.10), and 32.25 (21.55) kg.

From the large standard deviations in dry heartwood weight, it is evident that trees varied greatly in their heartwood content.

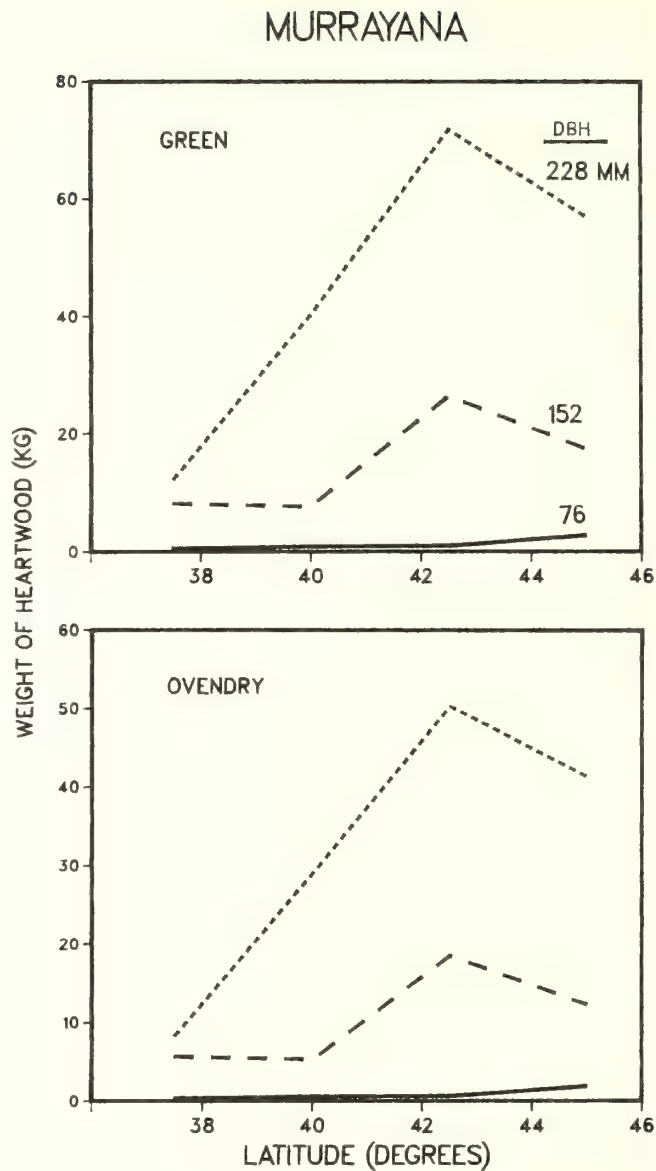


Figure 4-124—Weight of heartwood (green and ovendry) in *murrayana* trees of three diameters, related to latitude.

Ovendry Weight as Percentage of Stemwood—

Ovendried heartwood weight as a percentage of stemwood averaged lowest (9.16 percent) at 37.5 degrees and highest (23.16 percent) at 42.5 degrees latitude (fig. 4-125). The percentage was positively correlated with d.b.h., averaging 11.39 (11.05), 18.26 (11.91), and 21.52 (10.02) percent for trees of the three diameter classes.

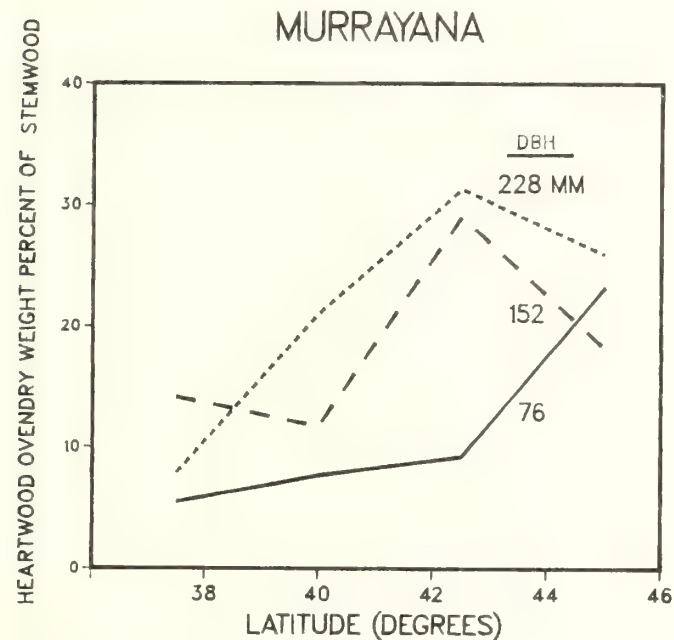


Figure 4-125—Heartwood as percentage of stemwood weight (ovendry basis) of *murrayana* trees of three diameters, related to latitude.

Stump-Root System, Wood Plus Bark

Specific Gravity—Specific gravity of wood plus bark of the stump-root system averaged 0.461, with standard deviation of 0.045. Average specific gravity was lowest (0.429) at 37.5 degrees latitude and highest (0.487) at 42.5 degrees, but was not significantly related to tree d.b.h. (fig. 4-126).

Weight, Green—Weight of wood plus bark of the green stump-root system was unrelated to latitude but was positively correlated with d.b.h., averaging 3.75 (1.07), 20.53 (5.36), and 43.87 (6.85) kg for trees of the three diameter classes.

Weight, Ovendry—On an ovendry basis trends were similar, with stump-root systems of trees of the three diameters averaging 1.80 (0.48), 9.70 (2.28), and 20.56 (3.82) kg.

Green Weight to Yield 1 m³ of Wood—The overall average of green weight of stump-root systems, wood plus bark, required to yield 1 m³ of wood was 1,109 kg, with standard deviation of 59 kg. This statistic varied inversely with d.b.h., averaging 1,156 (48), 1,110 (35), and 1,061 (50) kg for trees 76, 152, and 228 mm in d.b.h. It was not significantly related to latitude.

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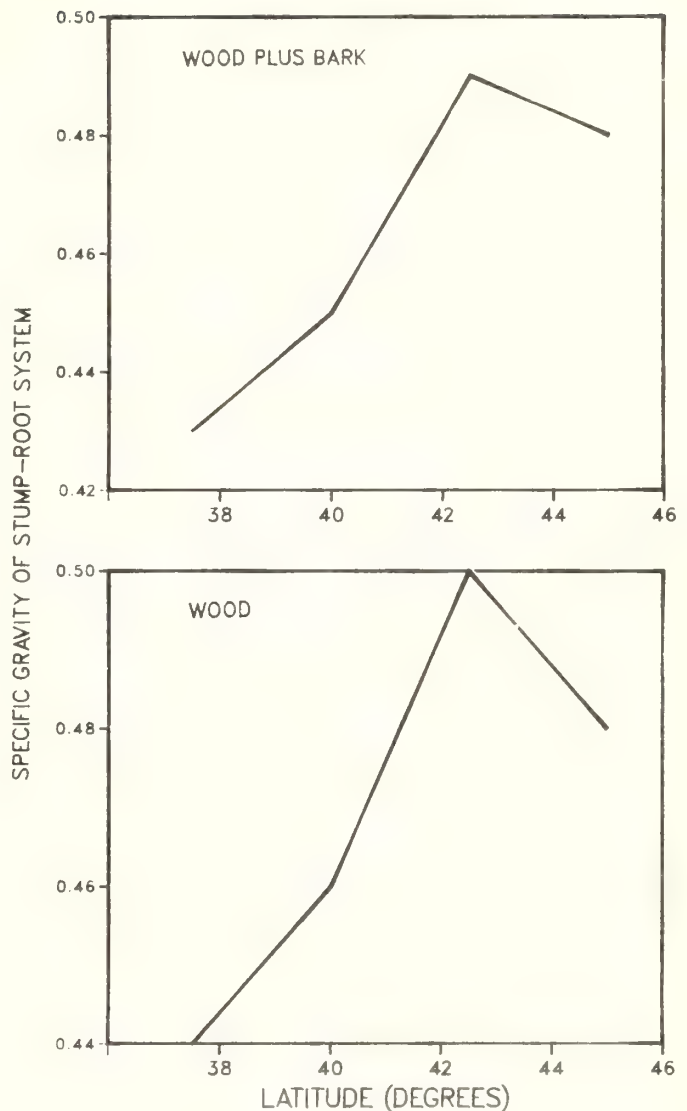


Figure 4-126—Specific gravity, based on ovendry weight and green volume, of the stump-root system (wood plus bark and wood only) of *murrayana* trees, related to latitude; diameter data pooled.

Tree Component Proportion, Green-Weight Basis—The stump-root system (wood plus bark) percentage of green weight of complete trees with foliage was smallest (10.39 percent) at 45 degrees and largest (15.76 percent) at 40 degrees latitude (fig. 4-127, top). This percentage was negatively correlated with d.b.h., averaging 15.63 (4.26), 14.02 (4.14), and 10.72 (2.19) percent for trees 76, 152, and 228 mm in d.b.h. The overall average was 13.18 percent, with standard deviation of 3.66 percentage points.

Tree Component Proportion, Owendry-Weight Basis—On an owendry-weight basis, latitudinal trends were similar (fig. 4-127, bottom), and trees of 76, 152, and 228 mm in d.b.h. averaged 15.05 (3.81), 13.82 (3.49), and 10.68 (2.21) percent of complete-tree owendry weight. The overall average was 13.18 percent, with standard deviation of 3.66 percentage points.

Stump-Root System, Wood Only

Specific Gravity—Specific gravity of wood of the stump-root system averaged 0.467, with standard deviation of 0.050. It was not significantly related to tree d.b.h., but did vary with latitude (fig. 4-126, bottom); specific gravity was minimum at 37.5 degrees (0.436) and maximum at 42.5 degrees (0.497).

Weight, Green—Weight of green wood of the stump-root system was unrelated to latitude but was positively correlated with d.b.h., averaging 3.16 (0.90), 18.14 (4.55), and 39.96 (6.16) kg for trees of the three diameter classes.

Weight, Owendry—On an owendry basis, d.b.h. was the only significant variable, with wood weight averaging 1.55 (0.42), 8.59 (2.03), and 18.73 (3.61) for trees 76 mm, 152 mm, and 228 mm in d.b.h.

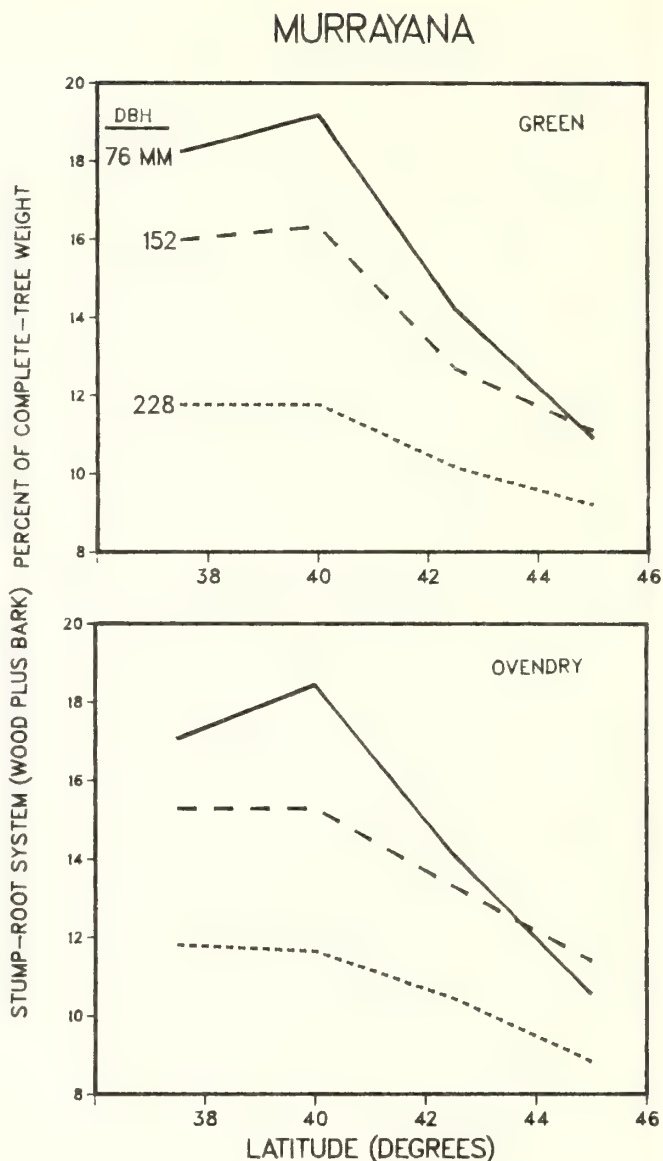


Figure 4-127—Stump-root system (wood plus bark) as percentage of the weight of complete trees with foliage—green and owendry—for *murrayana* trees of three diameters, related to latitude.

Stump-Root System, Bark Only

Specific Gravity—Specific gravity of bark of the stump-root system averaged 0.412, with standard deviation of 0.043. It did not vary significantly with latitude, but the larger trees had denser root-system bark than the smaller; that is, for trees 76, 152, and 228 mm in d.b.h., bark specific gravity averaged 0.386 (0.047), 0.429 (0.022), and 0.422 (0.046).

Weight, Green—Green weight of bark of the stump-root system averaged maximum at 40 degrees latitude and minimum at 45 degrees (fig. 4-128), and was positively correlated with d.b.h., averaging 0.59 (0.20), 2.39 (1.01), and 3.91 (1.05) kg for trees of the three diameter classes.

Weight, Ovendry—On an ovendry-weight basis, bark weight was not significantly related to latitude, but was positively correlated with d.b.h., averaging 0.25 (0.07), 1.12 (0.39), and 1.83 (0.46) kg for trees of the three diameter classes.

Stump-Root Bark as Percentage of Gross Stump-Root Weight, Green and Ovendry—Bark averaged 12.03 percent of the green weight of wood plus bark of the stump-root systems, with standard deviation of 3.56 percentage points. This percentage was unrelated to latitude, but was negatively correlated with d.b.h., averaging 15.72 (2.32), 11.47 (2.44), and 8.89 (1.71) percent for trees 76, 152, and 228 mm in d.b.h.

On an ovendry basis, bark weight proportion had overall average of 11.46 percent, with standard deviation of 2.96 percentage points. Trees 76, 152, and 228 mm in d.b.h. had 13.85 (1.85), 11.53 (2.77), and 9.00 (1.98) percent bark weight in stump-root systems.

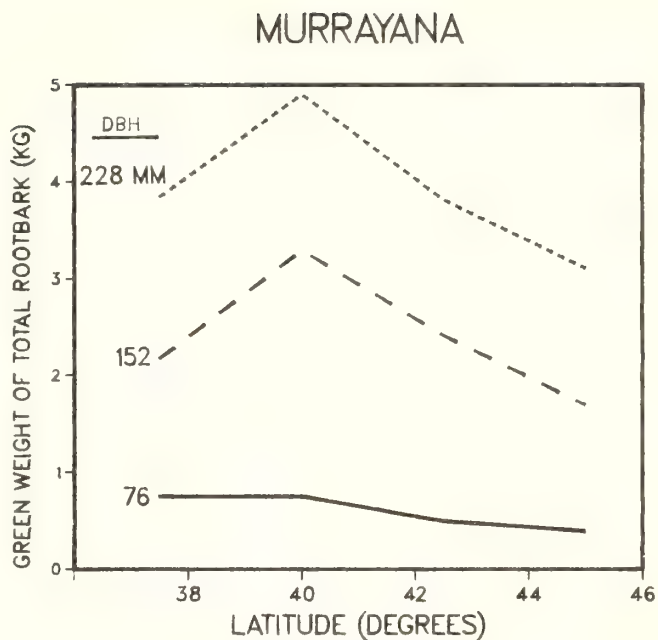


Figure 4-128—Weight of green bark from the stump-root system of *murrayana* trees of three diameters, related to latitude.

Stump, Wood Plus Bark

Specific Gravity—Specific gravity of stumps, wood plus bark, from groundline to 152-mm stump height averaged 0.496, with standard deviation of 0.054. It was unrelated to latitude but negatively correlated with d.b.h., averaging 0.520 (0.056), 0.506 (0.054), and 0.462 (0.033) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—Green weight of wood plus bark of stumps averaged maximum at 40 degrees latitude and minimum at 45 degrees (fig. 4-129, top). This weight was positively correlated with d.b.h., averaging 1.25 (0.38), 4.57 (1.68), and 6.80 (1.82) kg for trees of the three diameter classes.

Weight, Owendry—Owendry weight of wood plus bark of the stumps varied significantly only with d.b.h., averaging 0.65 (0.19), 2.30 (0.72), and 3.28 (0.83) kg for trees 76, 152, and 228 mm in d.b.h.

Stumpwood

Specific Gravity—Stumpwood had average specific gravity of 0.506, with standard deviation of 0.063. This specific gravity was unrelated to latitude, but was negatively correlated with d.b.h., averaging 0.541 (0.062), 0.512 (0.059), and 0.463 (0.042) for trees 76, 152, and 228 mm in d.b.h.

Weight, Green—Weight of green stumpwood was unrelated to latitude, but positively correlated with tree d.b.h., averaging 1.09 (0.32), 4.15 (1.54), and 6.27 (1.65) kg for the three diameter classes.

Weight, Owendry—Similarly, owendry stumpwood weight averaged 0.57 (0.17), 2.08 (0.67), and 2.98 (0.76) kg for trees of the three diameter classes.

Stumpbark

Specific Gravity—Specific gravity of stumpbark averaged 0.431, with standard deviation of 0.055. It was unrelated to latitude but positively correlated with d.b.h., averaging 0.398 (0.041), 0.445 (0.055), and 0.450 (0.057) for trees of the three diameter classes.

Weight, Green—Weight of green stumpbark averaged greatest at the southernmost latitude and least at the northernmost (fig. 4-129, bottom). Green stumpbark weight was positively correlated with d.b.h., averaging 160 (63), 415 (153), and 531 (201) g for trees of the three diameter classes.

Weight, Owendry—When owendry, stumpbark weight was not significantly related to latitude (although it averaged only 165 g at 40 degrees compared to an average of 234 g at 37.5 degrees). Dry stumpbark weight was positively correlated with d.b.h., averaging 72 (23), 222 (71), and 304 (111) g for trees of the three diameter classes.

MURRAYANA

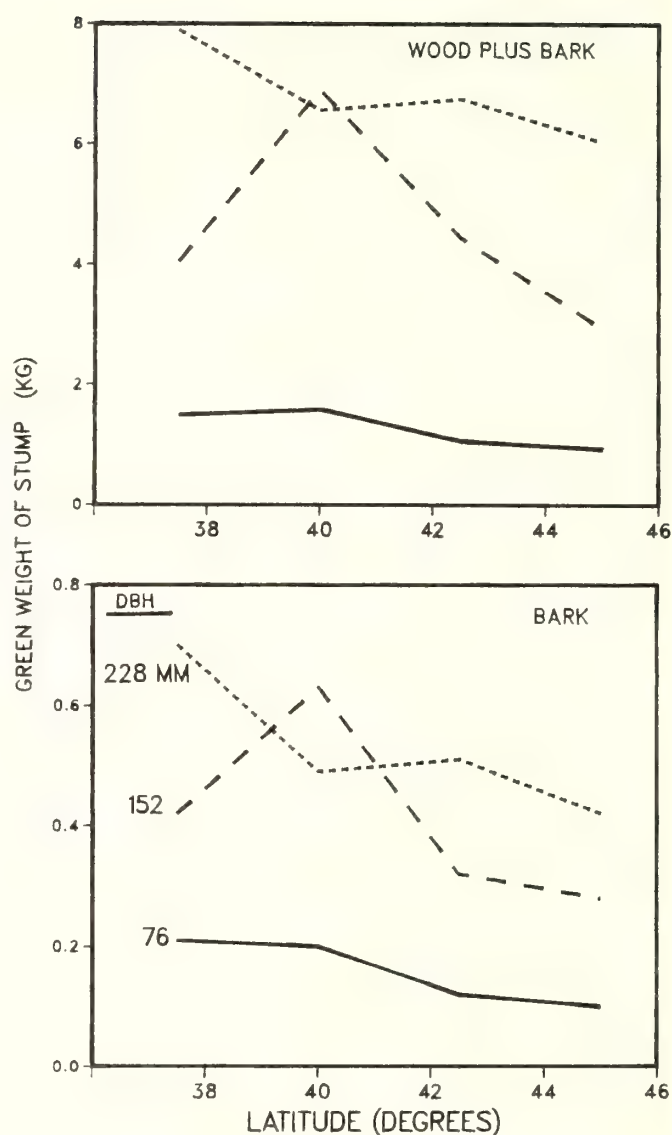


Figure 4-129—Weight of green stumps from groundline to 152-mm stump height (wood plus bark and bark only) of *murrayana* trees of three diameters, related to latitude.

Lateral Roots, Wood Plus Bark

Specific Gravity—Specific gravity of lateral roots, wood plus bark, was not significantly related to d.b.h. (although the average for 76-mm trees was 0.415 and that for 228 mm was 0.445, with 152-mm trees intermediate), and averaged 0.432, with standard deviation of 0.066. With diameter data pooled, specific gravity averaged lowest at 37.5 degrees (0.390) and highest (0.463) at 45 degrees (fig. 4-130).

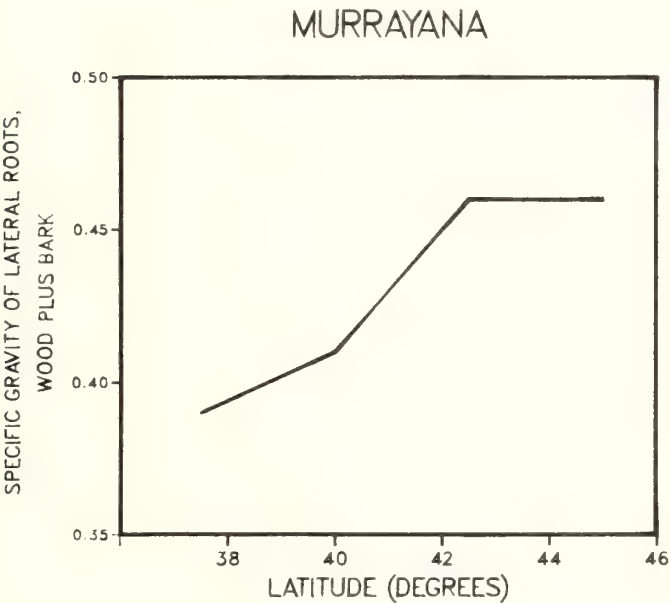


Figure 4-130—Specific gravity of wood plus bark of lateral roots (based on ovendry weight and green volume) of *murrayana* trees, related to latitude; diameter data pooled.

Weight, Green—Weight of wood plus bark of green lateral roots was highest at the two intermediate latitudes (fig. 4-131, top), and positively correlated with d.b.h., averaging 0.63 (0.27), 6.25 (2.45), and 15.66 (3.95) kg for trees of the three diameter classes.

Weight, Ovendry—Ovendry weight of wood plus bark of lateral roots varied similarly with latitude (fig. 4-131, bottom), and with d.b.h., averaging 0.28 (0.12), 2.80 (1.08), and 7.11 (1.80) kg for trees 76, 152, and 228 mm in d.b.h.

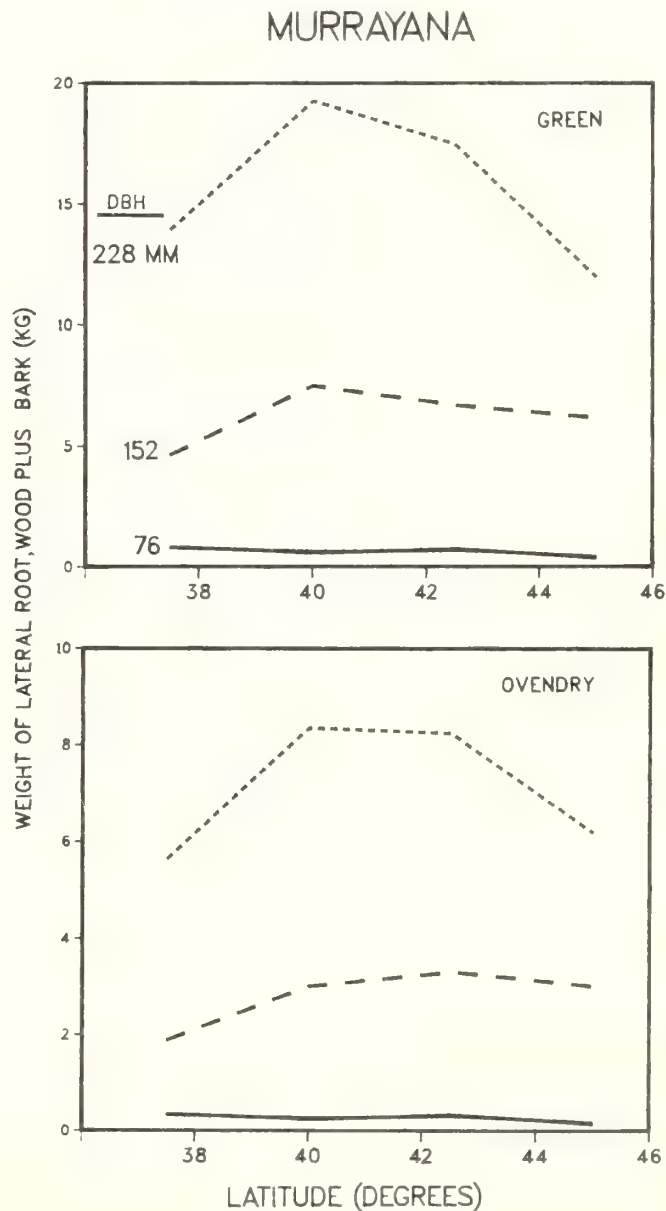


Figure 4-131—Weight of wood plus bark of lateral roots (green and ovendry) to a radius of 305 mm from stump pith from *murrayana* trees of three diameters, related to latitude.

Lateral Roots, Wood Only

Specific Gravity—Specific gravity of wood of lateral roots did not vary significantly with latitude or tree d.b.h.; the overall average was 0.443, with standard deviation of 0.072.

Weight, Green—Weight of green wood in lateral roots was unrelated to latitude, but was positively correlated with d.b.h., averaging 0.47 (0.21), 5.25 (1.94), and 13.79 (3.52) kg for trees of the three diameter classes.

Weight, Ovendry—Exhibiting similar trends, weight of ovendry wood of lateral roots averaged 0.21 (0.10), 2.38 (0.93), and 6.31 (1.72) kg for trees 76, 152, and 228 mm in d.b.h.

Lateral Roots, Bark Only

Specific Gravity—Specific gravity of bark of lateral roots was not significantly related to latitude or d.b.h.; the overall average was 0.388, with standard deviation of 0.059. Judging from the averages, however, a larger sample would likely have shown a positive correlation with d.b.h.

Weight, Green—Weight of green bark of lateral roots was highest at 40 degrees latitude and lowest at 45 degrees (fig. 4-132, top). It was positively correlated with d.b.h., averaging 164 (66), 998 (609), and 1,862 (707) g for trees 76, 152, and 228 mm in d.b.h.

Weight, Ovendry—On an ovendry-weight basis, the latitudinal trend was similar (fig. 4-132, bottom). Trees 76, 152, and 228 mm in d.b.h. had average weight of dry bark from lateral roots of 63 (22), 422 (204), and 801 (275) g.

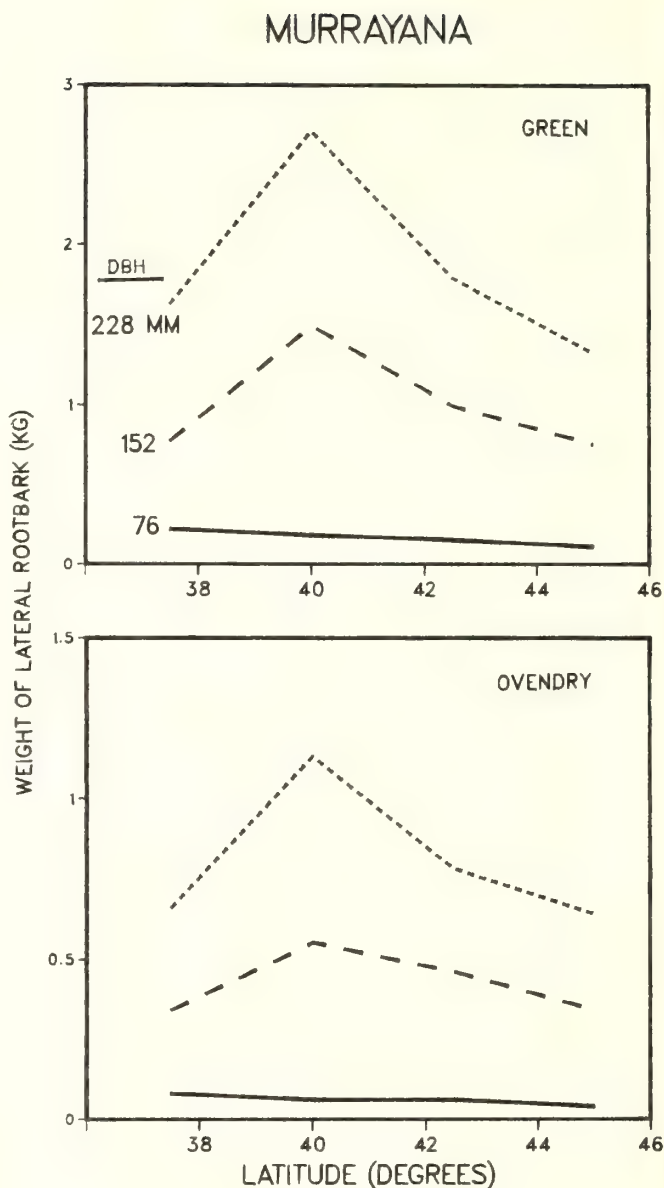


Figure 4-132—Weight of green and ovendry bark from lateral roots of *murrayana* trees of three diameters, related to latitude.

Central Root Mass-Taproot, Wood Plus Bark

Specific Gravity—Overall average specific gravity of wood plus bark of the central root mass-taproot was 0.457, with standard deviation of 0.051. It was unrelated to d.b.h., but varied with latitude—highest at 42.5 degrees and lowest at 37.5 degrees (fig. 4-133, top).

Weight, Green—Green weight of wood plus bark of the central root mass-taproot did not vary significantly with latitude, but was positively correlated with d.b.h., averaging 1.87 (0.68), 9.72 (2.65), and 21.40 (5.12) kg for trees of the three diameter classes.

Weight, Owendry—Owendry weights did not vary significantly with latitude, but were positively correlated with d.b.h., averaging 0.87 (0.30), 4.60 (1.24), and 10.17 (2.25) for trees 76, 152, and 228 mm in d.b.h.

Central Root Mass-Taproot, Wood Only

Specific Gravity—Overall average specific gravity of wood of the central root mass-taproot was 0.460, with standard deviation of 0.055. It did not vary significantly with d.b.h., but, with diameter data pooled, was maximum (0.502) at 42.5 degrees latitude and minimum (0.429) at 37.5 degrees (fig. 4-133, bottom).

Weight, Green—Weight of wood from the central root mass-taproot did not vary significantly with latitude, but was positively correlated with d.b.h., averaging 1.60 (0.58), 8.74 (2.36), and 19.90 (4.68) kg for trees of the three diameter classes.

Weight, Owendry—On an owendry-weight basis trends were similar, with wood weight averaging 0.76 (0.26), 4.13 (1.13), and 9.45 (2.03) kg for trees 76, 152, and 228 mm in d.b.h.

Central Root Mass-Taproot, Bark Only

Specific Gravity—Overall average specific gravity of bark of the central root mass-taproot was 0.426, with standard deviation of 0.057; it was not significantly related to latitude or to tree d.b.h. The latitudinal averages suggest a trend of increasing specific gravity from south (0.401) to north (0.464), however.

Weight, Green—Weight of green bark from the central root mass-taproot was unrelated to latitude but was positively correlated with d.b.h., averaging 271 (119), 975 (382), and 1,520 (549) g for trees 76, 152, and 228 mm in d.b.h.

Weight, Owendry—On an owendry-weight basis trends were similar, with bark weight averaging 113 (45), 471 (196), and 729 (296) g for trees of the three diameter classes.

MURRAYANA

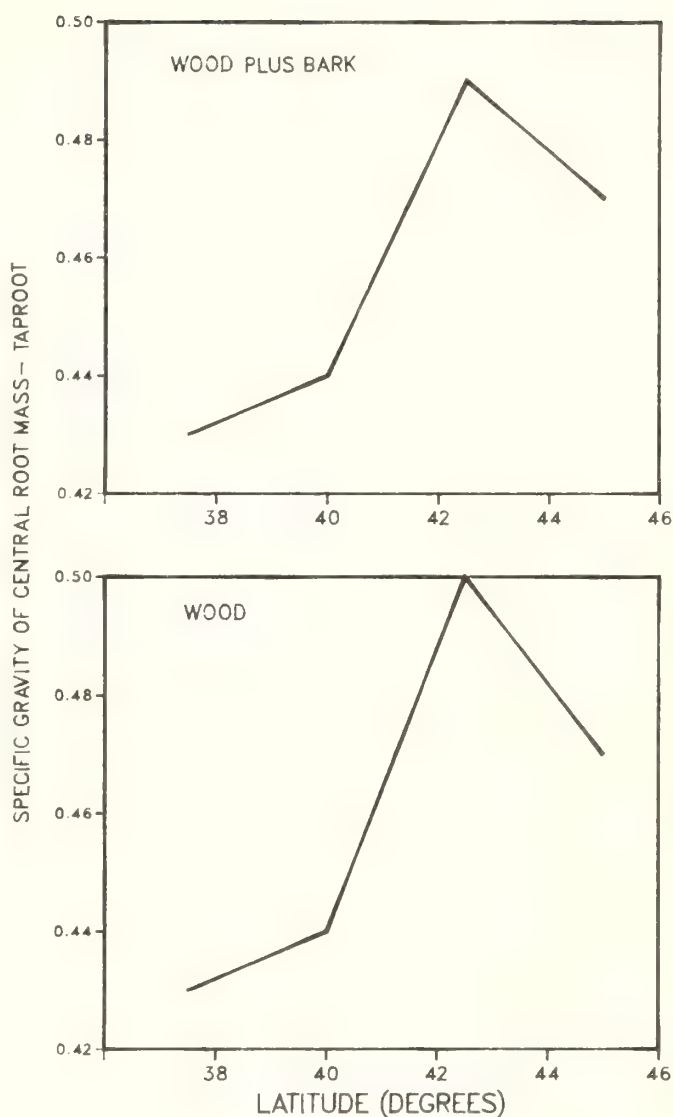


Figure 4-133—Specific gravity (based on owendry weight and green volume) of wood plus bark and wood only of the central root mass-taproot of *murrayana* trees, as related to latitude; diameter data pooled.

4-7 RESULTS—LATIFOLIA COMPARED TO MURRAYANA

The experimental design permitted an orthogonal comparison between the two varieties at three latitudes as follows:

Varieties:	(2)	<i>latifolia</i> and <i>murrayana</i>
D.b.h. classes:	(3)	76, 152, and 228 mm
Latitudinal zones:	(3)	40, 42.5, and 45 degrees
Elevational zones:	(1)	medium (1,148 to 2,711 m)
Replications:	(3)	

Sample size for this comparison therefore totaled 54 trees, 27 of each variety. In the discussion that follows, only significant relationships associated with varietal differences are graphed and tabulated; the other effects are more completely described in the preceding two sections.

Because specific gravity is a particularly useful statistic, table 4-11 lists component values that differ significantly at the three sample latitudes common to the two varieties. Throughout this table, *murrayana* components have higher specific gravities than those of *latifolia*.

Discussions of significant varietal differences in component weights, as well as specific gravities, follow.

Complete Tree Without Cones or Foliage

Complete-tree specific gravity of *murrayana* was higher than that of *latifolia* as follows (from table 4-11):

Component	<i>Latifolia</i>	<i>Murrayana</i>
Wood plus bark	0.406	0.446
Wood	.413	.456
Bark	.363	.387

Foliage

Latifolia had more weight of foliage, and a higher foliage-weight percentage, than *murrayana*, as follows:

D.b.h. and foliage moisture	<i>Latifolia</i>	<i>Murrayana</i>
----- kg/tree -----		
76 mm Green	2.48	1.71
Ovendry	1.12	.79
152 mm Green	12.53	7.93
Ovendry	5.96	3.79
228 mm Green	22.56	18.25
Ovendry	10.41	8.52

When green, foliage proportion of complete-tree weight averaged 7.4 percent for *latifolia* and 5.4 percent for *murrayana*, but at 42.5 degrees latitude the two varieties had about the same foliage proportion (fig. 4-134).

When ovendry, all three diameters of *latifolia* averaged higher in weight proportion of foliage (7.27 percent, with diameter data pooled) than *murrayana* (5.25 percent).

Table 4-11—Tree component specific gravities that differ significantly between *latifolia* and *murrayana* trees (at medium elevation and latitudes of 40, 42.5, and 45 degrees)¹

Tree component	Variety	
	<i>Latifolia</i>	<i>Murrayana</i>
Complete tree without cones or foliage		
Wood plus bark	0.406 (0.023)	0.446 (0.036)
Wood	.413 (.026)	.456 (.042)
Bark	.363 (.038)	.387 (.033)
Live branches		
Wood plus bark	.441 (.026)	.466 (.020)
Wood ²	.477 (.045)	.495 (.020)
Bark	.393 (.046)	.429 (.042)
Stem, tree average		
Wood plus bark ²	.395 (.024)	.441 (.039)
Wood ²	.401 (.027)	.451 (.046)
Heartwood ²	.427 (.035)	.500 (.072)
Stump-root system		
Bark	.390 (.064)	.418 (.041)
Stump, groundline to 152-mm height		
Wood plus bark	.472 (.048)	.505 (.052)
Wood	.479 (.056)	.516 (.060)
Bark ²	.417 (.079)	.433 (.056)
Central root mass-taproot		
Bark ²	.396 (.063)	.434 (.059)

¹Each value is based on ovendry weight and green volume data for 27 trees (that is, diameter data were pooled), and is followed by the standard deviation in parentheses.

²These component values are involved in significant interactions with d.b.h. or latitude; see text discussion.

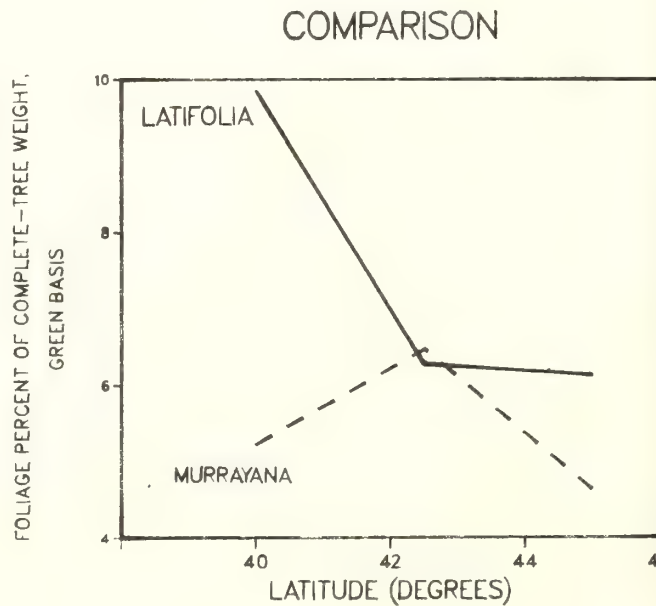


Figure 4-134—Foliage as percentage of complete-tree green weight; *latifolia* compared to *murrayana*, as related to latitude.

COMPARISON

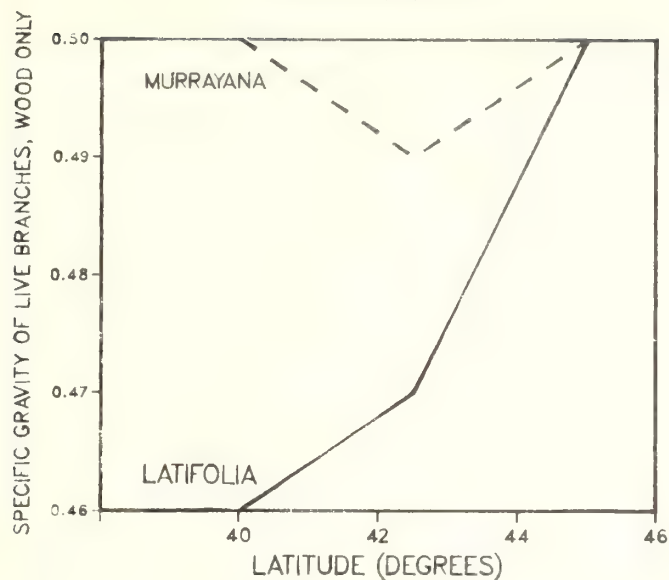


Figure 4-135—Specific gravity of live branch wood; *latifolia* compared to *murrayana*, as related to latitude.

COMPARISON

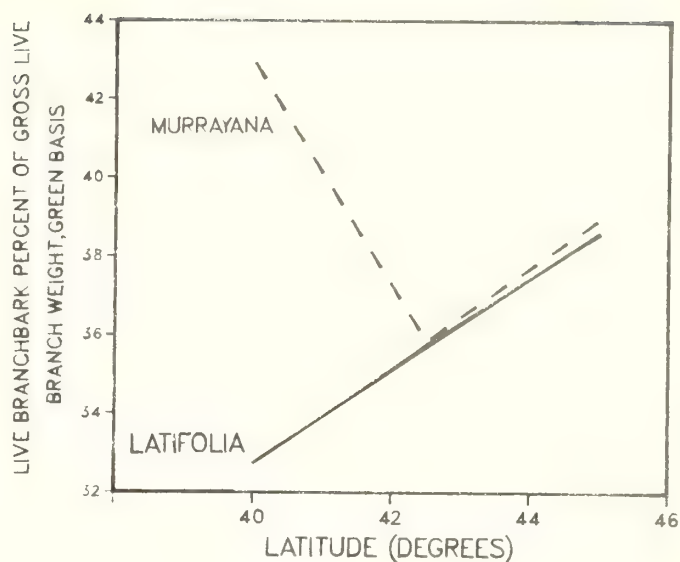


Figure 4-136—Live branchbark as percentage of green, foliage-free, live-branch weight; *latifolia* compared to *murrayana*, as related to latitude.

All Cones on Tree

The computed weight of cones per tree was greater on *latifolia* than on *murrayana*, as follows:

D.b.h. and foliage moisture	<i>Latifolia</i>	<i>Murrayana</i>
----- Grams -----		
76 mm Green	66	50
Ovendry	56	41
152 mm Green	601	210
Ovendry	524	177
228 mm Green	3,957	932
Ovendry	3,237	762

Live Branches

Live-branch specific gravity of *murrayana* was higher than that of *latifolia*, as follows (from table 4-11):

Component	<i>Latifolia</i>	<i>Murrayana</i>
Wood plus bark	0.441	0.466
Wood	.477	.495
Bark	.393	.429

Specific gravity of live-branch wood was about equal for the two varieties only at 45 degrees latitude (fig. 4-135).

For all three tree diameters, live branches of *murrayana* had a higher percentage of bark (39.2 percent) than *latifolia* (33.5 percent); the difference was greatest at 40 degrees latitude (fig. 4-136).

To yield 1 m³ of bark-free wood from live branches, a greater weight of green *murrayana* branches (1,631 kg) than *latifolia* branches (1,465 kg) is therefore required (fig. 4-137).

COMPARISON

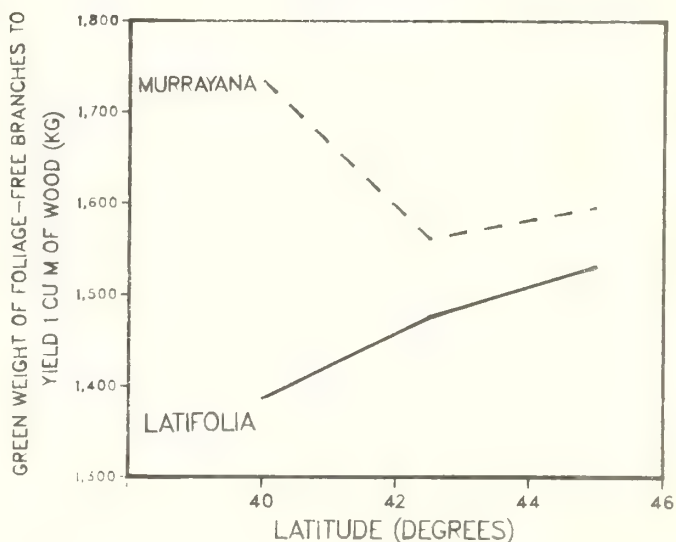


Figure 4-137—Green weight of foliage-free live branches to yield 1 m³ of wood; *latifolia* compared to *murrayana*, as related to latitude.

COMPARISON

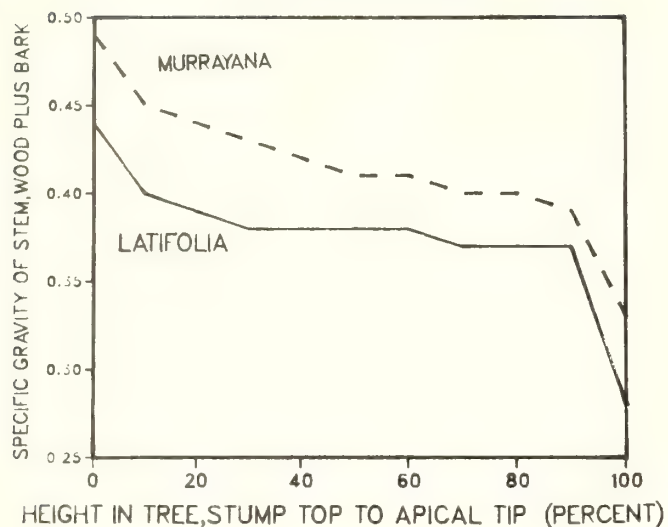


Figure 4-138—Specific gravity of stem (wood plus bark), oven-dry weight and green volume basis; *latifolia* compared to *murrayana*, as related to height in tree.

COMPARISON

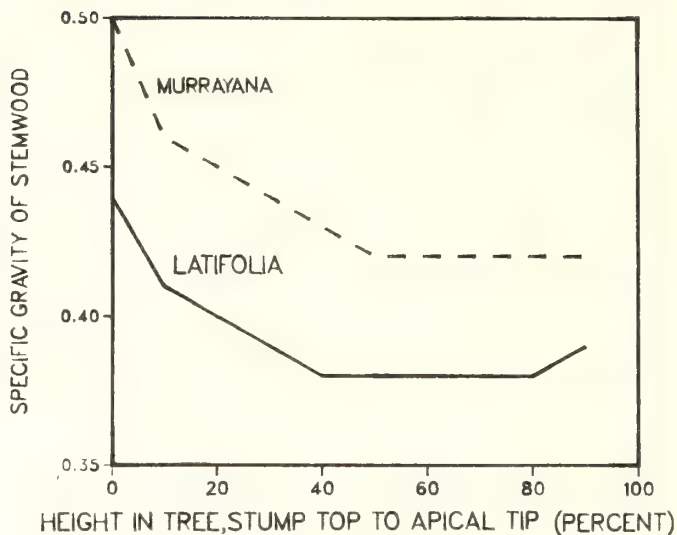


Figure 4-139—Specific gravity of stemwood, oven-dry weight and green volume basis; *latifolia* compared to *murrayana*, as related to height in tree.

Stem Specific Gravity

Wood Plus Bark—Specific gravity of wood plus bark of entire stems of *murrayana* averaged greater in trees of all three diameters than that of *latifolia*, as follows:

D.b.h.	<i>Latifolia</i>	<i>Murrayana</i>
mm		
76	0.398	0.466
152	.392	.444
228	.396	.412
Average	.395	.441

With diameter data pooled, the difference was observable at all percentages of tree heights (fig. 4-138).

Wood—Specific gravity of entire stemwood of *murrayana* was greater than that of *latifolia*, as follows:

D.b.h.	<i>Latifolia</i>	<i>Murrayana</i>
mm		
76	0.409	0.482
152	.396	.454
228	.398	.416
Average	.401	.451

With diameter data pooled, the difference was nearly constant at all percentages of tree height (fig. 4-139).

Heartwood of *murrayana* had average specific gravity greater than that of *latifolia*; the difference was less in large trees than in small, as follows:

D.b.h.	<i>Latifolia</i>	<i>Murrayana</i>
mm		
76	0.457	0.542
152	.419	.517
228	.404	.500
Average	.427	.500

COMPARISON

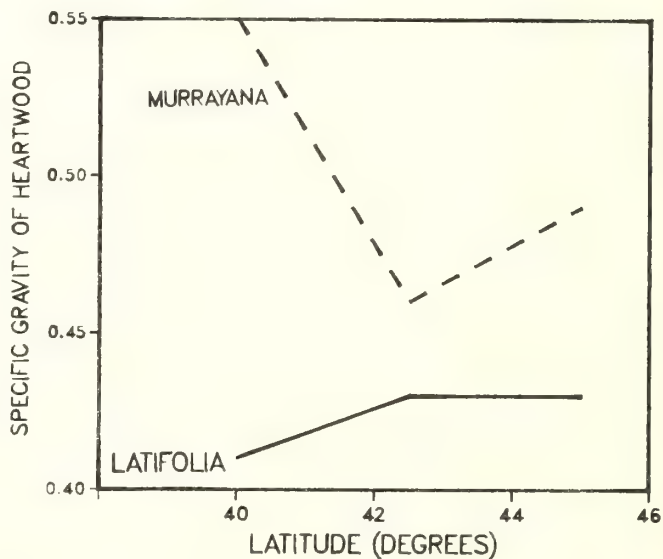


Figure 4-140—Specific gravity of heartwood, oven-dry weight and green volume basis; *latifolia* compared to *murrayana*, as related to latitude.

The difference was greatest at 40 degrees latitude (fig. 4-140).

COMPARISON

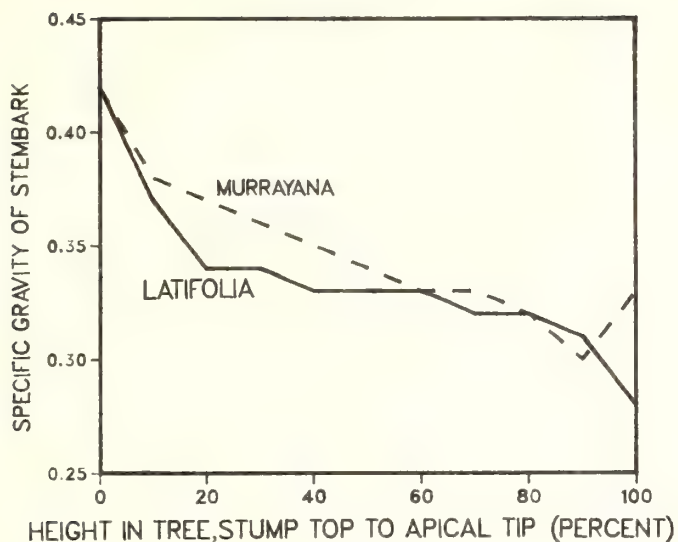


Figure 4-141—Specific gravity of stem bark, ovendry weight and green volume basis; *latifolia* compared to *murrayana*, as related to height in tree.

Bark—With diameter data pooled, stem bark specific gravity of *murrayana* was greater than that of *latifolia* at most heights in stems (fig. 4-141).

Stem Green Weight to Yield 1 m³ of Wood

With diameter data pooled, 1,025 kg of *murrayana* stems (wood plus bark, green) is required to yield 1 m³ of wood, whereas only 926 kg of *latifolia* will yield this volume of wood.

Stump-Root System

Wood Plus Bark—On both a green-weight and an ovendry-weight basis, *murrayana* trees averaged slightly higher in their percentage of complete-tree weight in the stump-root system than *latifolia*, as follows:

Moisture condition	<i>Latifolia</i>	<i>Murrayana</i>
	----- Percent -----	
Green	11.5	12.8
Ovendry	11.4	12.7

But the difference was reversed at 45 degrees latitude (figs. 4-142 and 4-143).

Bark—Bark of *murrayana* stump-root systems had average specific gravity of 0.418, that of *latifolia* only 0.390.

COMPARISON

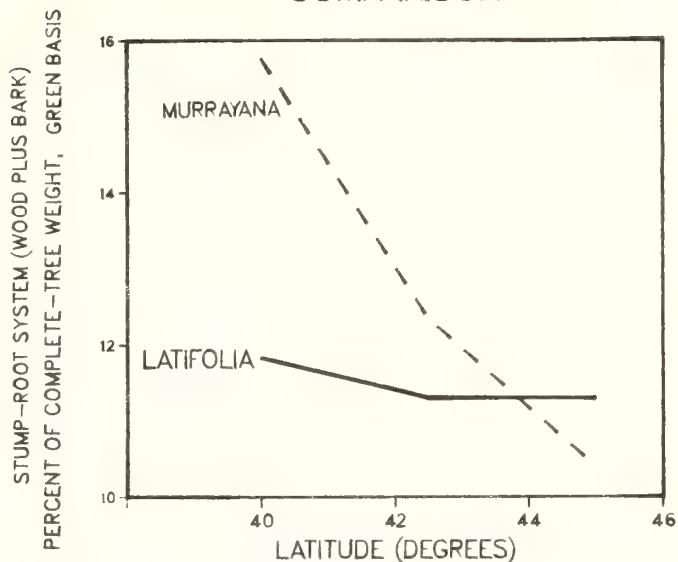


Figure 4-142—Stump-root system (wood plus bark) as percentage of green complete tree including foliage; *latifolia* compared to *murrayana*, as related to latitude.

COMPARISON

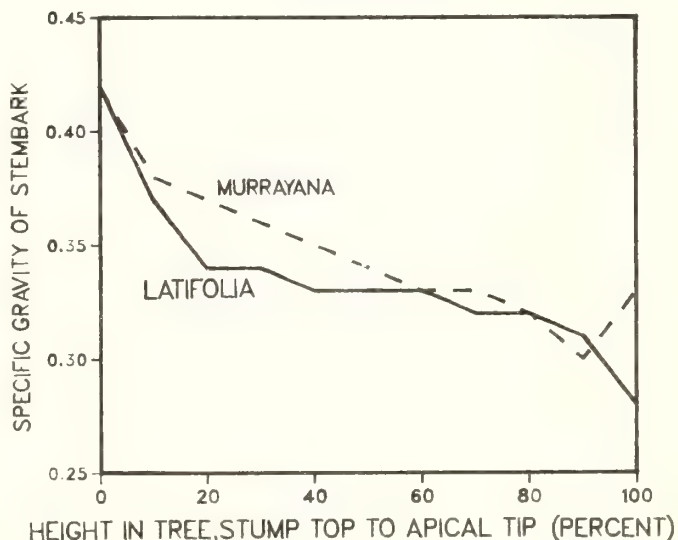


Figure 4-143—Stump-root system (wood plus bark) as percentage of ovendry complete tree including foliage; *latifolia* compared to *murrayana*, as related to latitude.

Stump

Wood Plus Bark—Specific gravity of wood plus bark of *murrayana* stumps from groundline to 152-mm top averaged 0.505, while that of *latifolia* was only 0.472.

Wood—*Murrayana* stumpwood specific gravity (0.516) was also higher than that of *latifolia* (0.479).

Relative green and dry weights of stumpwood of the two varieties varied with latitude and tree d.b.h. (figs. 4-144 and 4-145).

Bark—In smaller trees, stumpbark specific gravity was less in *latifolia* than in *murrayana*, as follows:

D.b.h.	<i>Latifolia</i>	<i>Murrayana</i>
mm		
76	0.346	0.412
152	.419	.440
228	.486	.448
Average	.417	.433

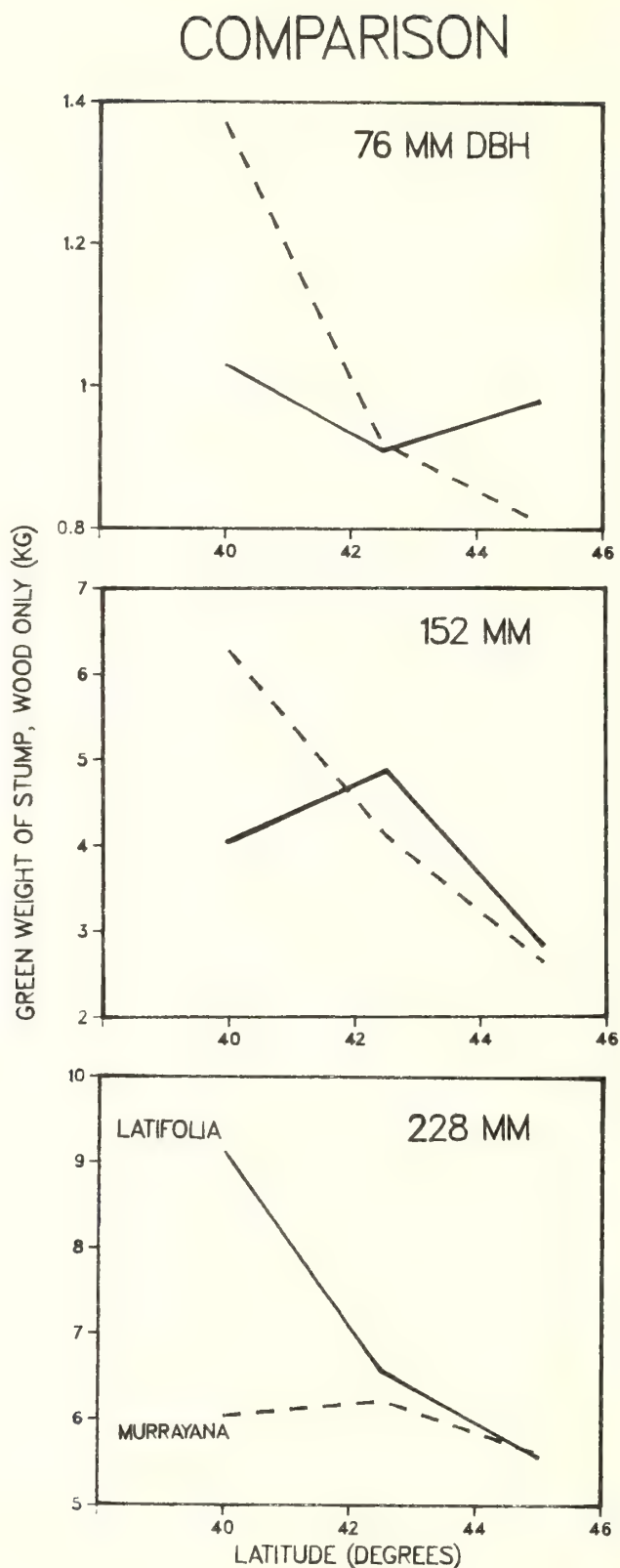


Figure 4-144—Green weight of stumpwood; *latifolia* compared to *murrayana*, as related to latitude.

COMPARISON

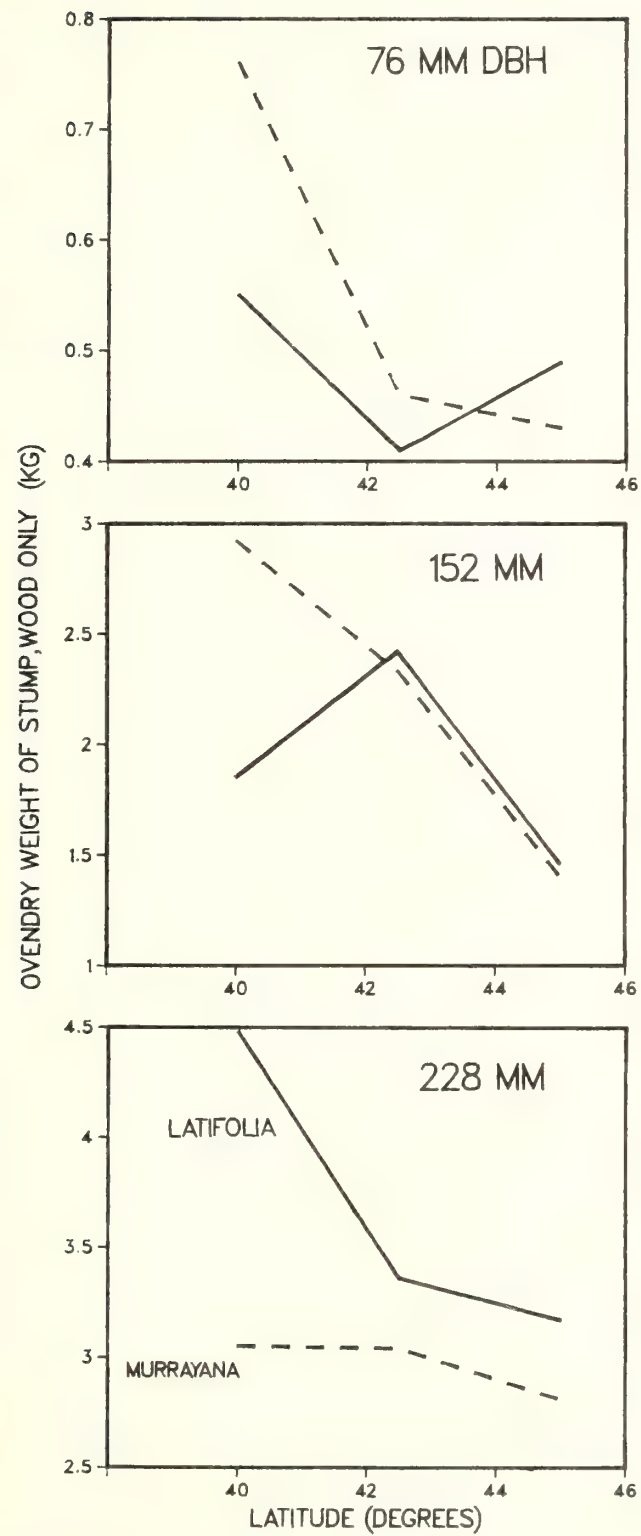


Figure 4-145—Ovendry weight of stumpwood; *latifolia* compared to *murrayana*, as related to latitude.

But bark of *latifolia* stumps generally weighed more than that of *murrayana*; not, however, in smaller trees at 40 degrees latitude (figs. 4-146 and 4-147).

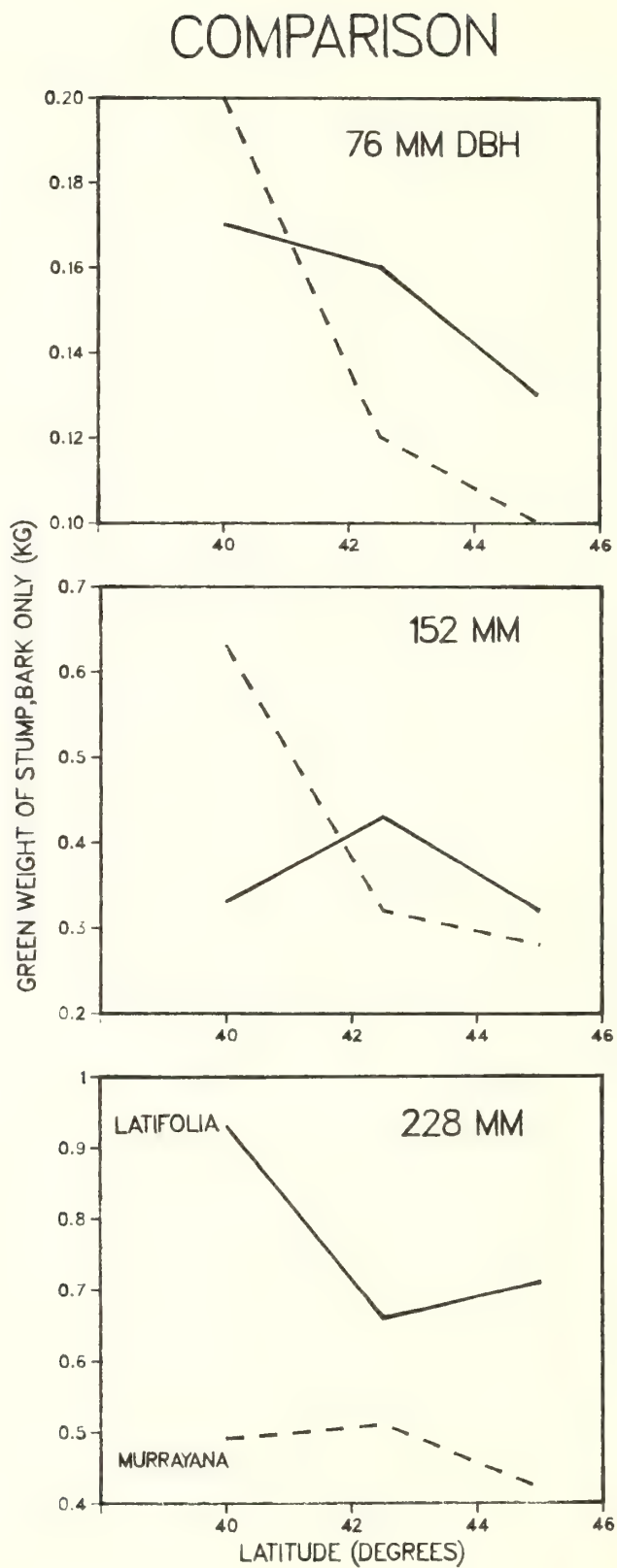


Figure 4-146—Green weight of stumpbark; *latifolia* compared to *murrayana*, as related to latitude.

COMPARISON

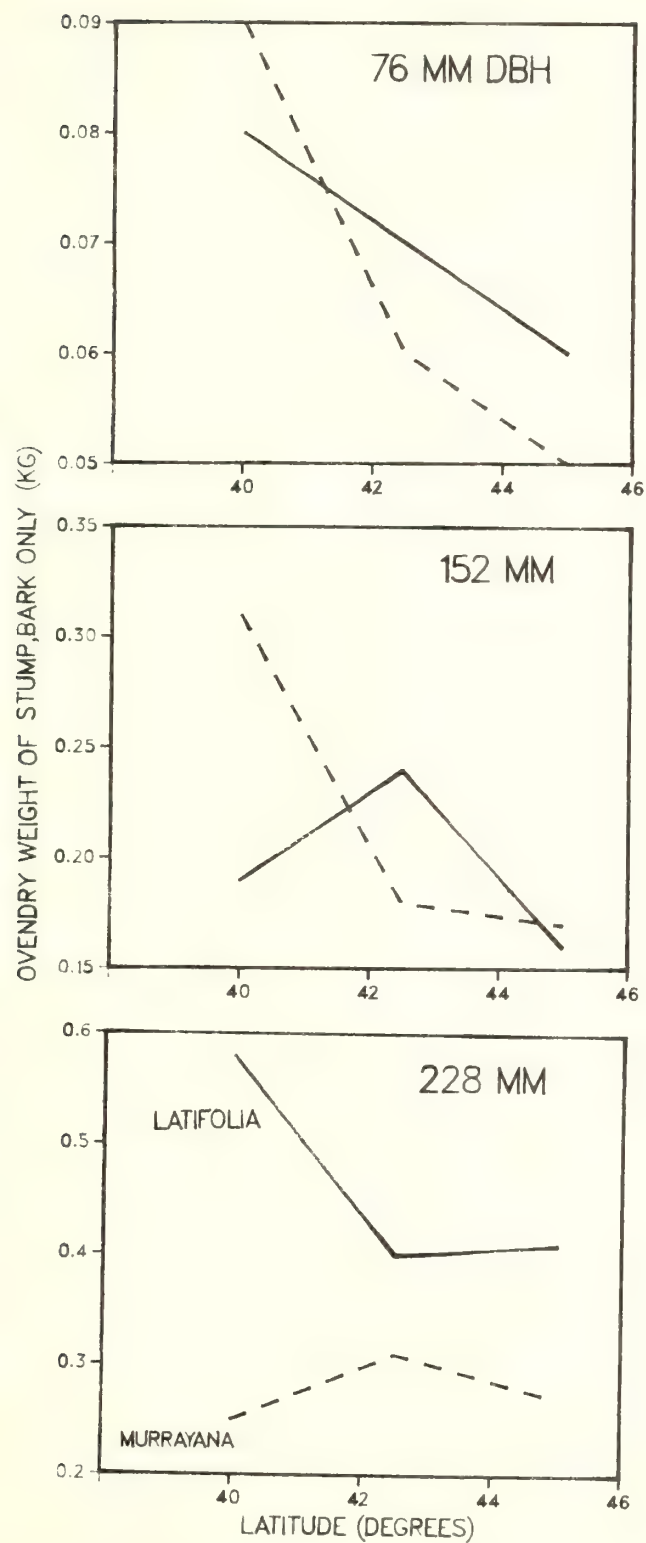


Figure 4-147—Ovendry weight of stumpbark; *latifolia* compared to *murrayana*, as related to latitude.

Central Root Mass-Taproot

Specific gravity of bark of the central root mass-taproot averaged higher in *murrayana* trees (0.434) than in *latifolia* (0.3967), but the relationship varied with latitude (fig. 4-148).

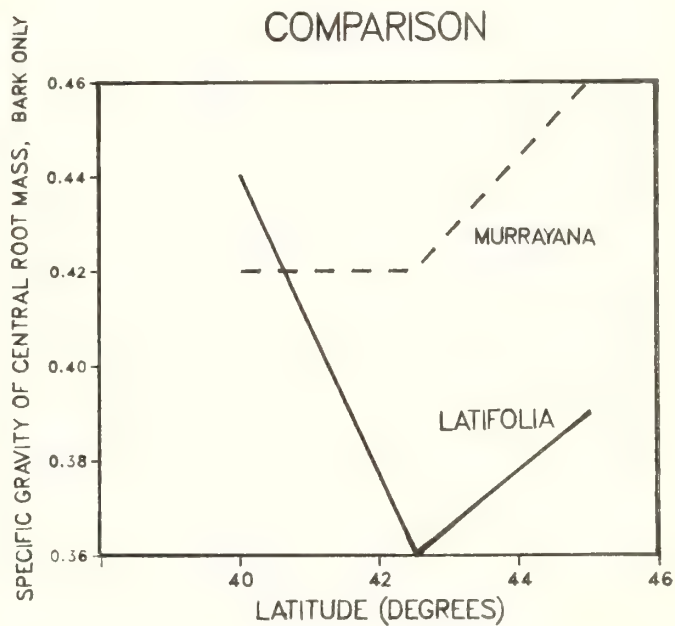


Figure 4-148—Specific gravity of bark of the central root mass-taproot, ovendry weight and green volume basis; *latifolia* compared to *murrayana*, as related to latitude.

4-8 SUMMARY OF RESULTS

Specific Gravity

The most important finding of this research is that stemwood specific gravity of *latifolia* trees 76, 152, and 228 mm in d.b.h.—in a spectrum of ages—decreased with increasing d.b.h. and increased with increasing latitude. With diameter, latitudinal, and elevational data pooled, *latifolia* stemwood specific gravity averaged 0.418 (sapwood averaged 0.414 and heartwood 0.434), based on oven-dry weight and green volume. As noted above, *latifolia* stemwood specific gravity was negatively correlated with d.b.h., averaging 0.427, 0.419, and 0.407 for trees 76, 152, and 228 mm in d.b.h. Trees in the three diameter classes averaged 71, 91, and 107 years old, respectively, with growth-ring width at a stump height of 152 mm averaging 0.67, 1.01, and 1.33 mm.

Stemwood specific gravity diminished with increasing height in tree up to the base of the live crown, above which it remained constant or increased slightly at values between 0.39 and 0.40. At all percentages of height in the stems, small-diameter trees had higher stemwood specific gravity than large trees. For all diameters, entire stemwood specific gravity could be closely estimated from stemwood specific gravity at 20 percent of tree height. Stemwood specific gravity was unrelated to elevational zone, but was positively correlated with latitude, averaging minimum (0.390) at 42.5 degrees and maximum (0.435) at 55 degrees. The specific gravity trend was inverse to stemwood moisture content trend with latitude, and aligned with the trend of heartwood as a percentage of stemwood weight.

Wood of *latifolia* live branches had higher average specific gravity (0.487) than that of the stump-root system (0.469) or stem (0.418). Specific gravity of bark of live branches, stump-root system, and stem averaged 0.411, 0.415, and 0.369, respectively.

Complete-Tree Weight, Including Foliage

Complete *latifolia* trees 76, 152, and 228 mm in d.b.h. had average oven-dry weights of 28, 170, and 440 kg, including foliage and stump-root systems to a lateral-root radius of 305 mm from stump pith. Trees from high-elevation zones weighed less than those from low. With diameter and elevational data pooled, trees weighed least in the three southernmost latitudes (40 through 45 degrees) and most in latitudes 47.5 through 55 degrees.

Tree Component Proportions of Complete-Tree Oven-dry Weight

Latifolia tree component proportions varied significantly with d.b.h., latitude, and elevation; but with all data pooled, component weight percentages (oven-dry) averaged 6.8, 1.0, 5.9, 2.0, 72.8, and 11.5 percent for technical foliage, cones, live branches, dead branches, stem, and stump-root system. Small trees had a greater proportion of foliage and stump-root system, and a lesser proportion of cones, live branches, and stem weight than large trees.

Weight of Green Components for 1 m³ of Wood

The weight of *latifolia* green wood plus bark of the three major tree components required to provide 1 m³ of bark-free wood was greater for small trees than large, and varied with latitude and elevation. With all data pooled, average requirements for foliage-free branches, stem (152-mm stump height to apical tip), and stump-root system were 1,448, 920, and 1,046 kg, respectively.

Proportion of Bark in Each Component, Oven-dry-Weight Basis

Bark oven-dry-weight proportions of tree components were greater in small trees than large, and varied with latitude and elevational zone. With all *latifolia* data pooled, however, averages were 11.6, 10.1, 33.8, and 12.5 percent for complete foliage-free tree, stem, live branches, and stump-root system, respectively.

Longitudinal Effects

Variations related to longitudinal zones across latitudinal sampling zones were minor, except that individual *latifolia* cones from trees on the east end of sampling zones weighed more than those on trees from the west end.

Latifolia Compared to *Murrayana*

The text reports specific gravity and weight data for *murrayana* at medium elevation from four latitudes—37.5, 40, 42.5, and 45 degrees. Of these latitudes, *latifolia* was sampled from 40, 42.5, and 45 degrees, so a comparison at medium elevation at these three latitudes was possible based on 27 trees of each variety—nine trees 76 mm, nine 152 mm, and nine 228 mm in d.b.h.

At these three latitudes *murrayana* had higher specific gravity for most tree components than *latifolia*; for example, stemwood of *murrayana* averaged 0.451 vs. 0.401 for *latifolia*, and specific gravity of bark of complete trees averaged 0.387 for *murrayana* vs. 0.363 for *latifolia* (basis of oven-dry weight and green volume).

Latifolia had more weight of foliage per tree, and a higher foliage-weight proportion (7.3 percent vs. 5.3 percent, oven-dry basis).

With diameter data pooled, 1,025 kg of *murrayana* stems (wood plus bark, green) is required to yield 1 m³ of bark-free wood; whereas only 926 kg of *latifolia* will yield this volume of wood.

4-9 REFERENCES

- Adamovich, L. L. Engineering characteristics of Canadian trees—centre of gravity and green weight of components of four species in interior British Columbia. Information Report FMR-X-74. Ottawa, ON: Department of the Environment, Canadian Forestry Service, Forest Management Institute; 1975. 55 p.

- Agee, James K. Fuel weights of understory-grown conifers in southern Oregon. *Canadian Journal of Forest Research*. 13(4): 648-656; 1983.
- American Lumberman. Properties, preparation and increasing utilization of lodgepole pine. *American Lumberman*. 1851: 39; 1910 November 12.
- Baranyay, J. A.; Szabo, T.; Hunt, K. Effect of *Atropellis* canker on growth and utilization of lodgepole pine. Information Report BC-X-86. Victoria, BC: Department of the Environment, Canadian Forestry Service, Pacific Forest Research Centre; 1973. 22 p.
- Benson, Robert E. Management consequences of alternative harvesting and residue treatment practices—lodgepole pine. General Technical Report INT-132. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1982. 58 p.
- Bjorklund, Tarja. Kontortamännyn puutekniset ominaisuudet: Technical properties of lodgepole pine wood. *Folia Forestalia*. 522: 1-25; 1982.
- Bramhall, G.; Wellwood, R. W. Kiln drying of western Canadian lumber. Information Report VP-X-159. Vancouver, BC: Department of Fisheries and the Environment, Canadian Forestry Service, Western Forest Products Laboratory; 1976. 112 p. Available from: FORINTEK CANADA CORP., Vancouver, BC.
- Brazier, J. D. A report on the effects of provenance on the timber properties of lodgepole pine. In: *Pinus contorta* as an exotic species: Proceedings, IUFRO working party meeting on *Pinus contorta* provenances (S2-02-06) in Norway and Sweden; 1980. Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics; 1980: 181-207.
- Brown, James K. Weight and density of crowns of Rocky Mountain conifers. Research Paper INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1978. 56 p.
- Brown, James K.; Snell, J. A. Kendall; Bunnell, David L. Handbook for predicting slash weight of western conifers. General Technical Report INT-37. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1977. 35 p.
- Cannell, M. G. R.; Sheppard, L. J.; Ford, E. D.; Wilson, R. H. F. Clonal differences in dry matter distribution, wood specific gravity and foliage "efficiency" in *Pinus sitchensis* and *Pinus contorta*. *Silvae Genetica*. 32(5-6): 195-202; 1983.
- Carlson, T. C.; Nimlos, T. J. Using soil series to predict site index and wood specific gravity in western Montana. *Northwest Science*. 40(2): 56-67; 1966.
- Chapman, R. C.; Baldwin, V. C.; Clausnitzer, R. R. Cubic foot volume, bole green weight and total above ground green weight of small diameter lodgepole pine, larch and ponderosa pine. Research Bulletin XB 0914. Pullman, WA: Washington State University, Agricultural Research Center; 1982. 7 p.
- Dobie, J.; McIntosh, J. A. Spruce foliage yields more than triple that of pine. *Pulp & Paper of Canada*. 77(10): 71-72; 1976.
- Echols, R. M. Uniformity of wood density assessed from x-rays of increment cores. *Wood Science Technology*. 7(1): 34-44; 1973.
- Fahey, Thomas D. Evaluating dead lodgepole pine for products. *Forest Products Journal*. 30(12): 34-39; 1980.
- Fahey, Thomas D. Value ranking for utilizing lodgepole pine residues. In: Harvesting and utilization opportunities for forest residues in the Northern Rocky Mountains: symposium proceedings; 1979 November 28-30; Missoula, MT. General Technical Report INT-110. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981: 239-250.
- Fahey, Timothy J. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecological Monographs*. 53(1): 51-72; 1983.
- Fahnestock, George R.; Dieterich, John H. Logging slash flammability after five years. Research Paper 70. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1962. 15 p.
- Forest Products Research Laboratory, Princes Risborough. Properties of thinnings of home-grown lodgepole pine (*Pinus contorta*): progress report 2—consignment 1027; 1960. 34 p.
- Foulger, A. N.; Harris, Johnny. Volume of wood, bark and needles after clearcutting a lodgepole pine stand. *Journal of Forestry*. 71(2): 93-95; 1973.
- Hakkila, Pentti; Panhelainen, Arja. On the wood properties of *Pinus contorta* in Finland. *Communications Instituti Forestalis Fenniae*. 73(1); 1970. 43 p.
- Harris, J. Maddern. Physical properties, resin content, and tracheid length of lodgepole pine grown in New Zealand. *New Zealand Journal of Forest Science*. 3(1): 91-109; 1973.
- Heger, L. Longitudinal variation of specific gravity in stems of black spruce, balsam fir, and lodgepole pine. *Canadian Journal of Forest Research*. 4(3): 321-326; 1974.
- Henderson, J.; Petty, J. A. A comparison of wood properties of coastal and interior provenances of lodgepole pine. *Forestry (Great Britain)*. 45(1): 49-57; 1972.
- Johnstone, W. D. Some variations in specific gravity and moisture content of 100-year-old lodgepole pine trees. Information Report A-X-29. Calgary, AB: Department of Fisheries and Forestry, Canadian Forestry Service, Forest Research Laboratory; 1970a. 19 p.
- Johnstone, W. D. Component dry weights of 100-year-old lodgepole pine trees. Information Report A-X-31. Calgary, AB: Department of Fisheries and Forestry, Canadian Forestry Service, Forest Research Laboratory; 1970b. 14 p.
- Johnstone, W. D. Total standing crop and tree component distributions in three stands of 100-year-old lodgepole pine. In: Forest biomass studies: proceedings of working group on forest biomass studies: section 25, growth and yield; 15th IUFRO Congress; 1971 March 15-20; Gainesville, FL. Miscellaneous Report 132. Orono, ME: University of Maine, Life Sciences and Agriculture Experiment Station; 1971: 81-89.

- Kaufmann, Merrill R.; Troendle, Charles A. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *Forest Science*. 27(3): 477-482; 1981.
- Kiil, A. D. Weight of the fuel complex in 70-year-old lodgepole pine stands of different densities. Department Publication 1228. Ottawa, ON: Canada Department of Forestry and Rural Development, Forestry Branch; 1968. 9 p.
- Maeglin, Robert R.; Wahlgren, Harold E. Western wood density survey: report No. 2. Research Paper FPL 183. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory; 1972. 24 p.
- Moir, W. H.; Francis, R. Foliage biomass and surface area in three *Pinus contorta* plots in Colorado. *Forest Science*. 18(1): 41-45; 1972.
- Moir, William H. Litter, foliage, branch, and stem production in contrasting lodgepole pine habitats of the Colorado Front Range. In: Franklin, Jerry F.; Dempster, L. J.; Waring, Richard H., eds. *Proceedings—research on coniferous forest ecosystems—a symposium*; 1972 March 23-24; Bellingham, WA. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1972: 189-198.
- Moore, Musser Beighley. Geographic variation in lodgepole pine in the Central Rocky Mountains. Fort Collins, CO: Colorado State University; 1981. 188 p. Ph.D. dissertation. Available from: University Microfilms International, Ann Arbor, MI.
- Muraro, S. J. Lodgepole pine logging slash. Department of Forestry Publication 1153. Ottawa, ON: Department of Forestry Canada; 1966. 14 p.
- Muraro, S. J. The lodgepole pine fuel complex. Information Report BC-X-53. Victoria, BC: Department of the Environment, Canadian Forestry Service, Pacific Forest Research Centre; 1971. 50 p.
- Okkonen, E. A.; Wahlgren, H. E.; Maeglin, R. R. Relationships of specific gravity to tree height in commercially important species. *Forest Products Journal*. 22(7): 37-42; 1972.
- Pearson, John Alan. Biomass distribution and ecosystem development in lodgepole pine forests of the Medicine Bow Mountains, Wyoming. Laramie, WY: University of Wyoming; 1982. 113 p. Ph.D. dissertation.
- Peterson, E. B.; Levson, V. M.; Kabzems, R. D. Upper limits of standing crop density for woody species in the prairie provinces. Information Report NOR-X-243. Edmonton, AB: Environment Canada, Canadian Forestry Service, Northern Forest Research Centre; 1982. 55 p.
- Reynolds, James F.; Knight, Dennis H. The magnitude of snowmelt and rainfall interception by litter in lodgepole pine and spruce-fir forests in Wyoming. *Northwest Science*. 47(1): 50-60; 1973.
- Roydhouse, F. M.; Crane, J. L.; Bassman, J. H. Biomass distribution in young stands of stagnant and non-stagnant lodgepole pine. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. *Lodgepole pine: the species and its management: symposium proceedings*; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Washington State University, Office of Conferences and Institutes, Cooperative Extension; 1985: 379. Abstract.
- Running, Steven W. Relating plant capacitance to the water relations of *Pinus contorta*. *Forest Ecology and Management*. 2(4): 237-252; 1980.
- Singh, T. Biomass equations for ten major tree species of the prairie provinces. Information Report NOR-X-242; ENFOR Project P-92. Edmonton, AB: Environment Canada, Canadian Forestry Service, Northern Forest Research Centre; 1982a. 34 p.
- Singh, T. Weight tables for important tree species in the prairie provinces. Forest Management Note 14. Edmonton, AB: Environment Canada, Canadian Forestry Service, Northern Forest Research Centre; 1982b. 4 p.
- Singh, T. Variation in the oven-dry wood density of ten prairie tree species. *Forestry Chronicle*. 60(4): 217-221; 1984.
- Smith, J. H. G.; DeBell, D. S. Opportunities for short rotation culture and complete utilization of seven northwestern tree species. *Forestry Chronicle*. 49(1): 31-34; 1973.
- Smith, J. H. G.; Kozak, A. Thickness, moisture content, and specific gravity of inner and outer bark of some Pacific Northwest trees. *Forest Products Journal*. 21(2): 38-40; 1971.
- Smythe, Stuart L. Comparative characteristics of lodgepole pine (*Pinus contorta*) wood parasitized by dwarfmistletoe (*Arceuthobium americanum*). *Journal of the Colorado-Wyoming Academy of Science*. 5(8): 66-67; 1967. Abstract.
- Snell, J. A. Kendall; Brown, James K. Handbook for predicting residue weights of Pacific Northwest conifers. General Technical Report PNW-103. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1980. 44 p.
- Snell, J. A. Kendall; Max, Timothy A. Bark-to-wood ratios for logging residue in Oregon, Washington, and Idaho. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1982. 9 p. Administrative report.
- Sylvander, Robert B.; Smith, J. Harry G. Widths and specific gravity of earlywood and latewood components of annual rings from interior British Columbia lodgepole pine. Vancouver, BC: University of British Columbia, Faculty of Forestry; 1973. 61 p.
- Tackle, David. Specific gravity of lodgepole pine in the Intermountain Region. Research Note 100 (rev.). Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1962. 4 p.
- Taylor, Fred W.; Wang, Eugene I. C.; Micko, Michael M. Differences in the wood of lodgepole pine in Alberta. *Wood and Fiber*. 14(4): 296-309; 1982.
- U.S. Department of Agriculture, Forest Service. Wood handbook: wood as an engineering material. Agriculture Handbook 72, rev. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory; 1974. 415 p.
- Weaver, T.; Forcella, F. Biomass of fifty conifer forests and nutrient exports associated with their harvests. *Great Basin Naturalist*. 37(3): 395-401; 1977.

CHAPTER 5: DISTRIBUTION, MOISTURE CONTENT, WEIGHT, AND SPECIFIC GRAVITY OF HEARTWOOD AND SAPWOOD

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5-1 INTRODUCTION

The sapwood of stem and branches changes abruptly after a particular, but variable, age. The resulting interior core is heartwood; that is, the inner zone of wood which, in the growing tree, has ceased to contain living cells and in which the reserve materials (for example, starch) have been removed or converted into heartwood substances. Heartwood in lodgepole pine is usually darker than sapwood.

In lodgepole pine, sapwood and heartwood differ not only in color, but in extractive content, moisture content, specific gravity, and permeability. Processors of lodgepole pine stemwood therefore should find it useful to know something of the gross dimensions, moisture contents, weights, and specific gravities of these two stem components.

5-2 OBJECTIVE AND SCOPE

Parameters describing heartwood and sapwood distribution, moisture content, weight, and specific gravity are discussed in this chapter, but no attempt is made to construct equations predicting these parameters. Instead, graphs are presented of data aggregated in various significant ways that permit reading of the parameters directly from observed study data.

As previously noted, the entire characterization effort is confined to two varieties of lodgepole pine: *Pinus contorta* var. *latifolia* Engelm. and *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm., with emphasis on the former. The primary objective during tree collection was to obtain three replications of disease- and insect-free specimens of var. *latifolia* measuring 76, 152, and 228 mm in diameter at breast height (d.b.h.) at low, medium, and high elevations from nine equally spaced north latitudinal zones (40 to 60 degrees) across 10 degrees of longitude in such a way as to encompass the major range of this variety (fig. 1-1).

A secondary objective was to sample three replications of these same three diameter classes of var. *murrayana* at midelevation at four north latitudes (37.5, 40, 42.5, and 45 degrees) in California and Oregon at a single longitude per latitude (fig. 1-1).

The trees of both varieties were sampled in such a way that between-variety comparisons could be made for midelevation trees at latitudes 40, 42.5, and 45 degrees. The sampling plan does not permit computation of species-average values. The collection totaled 243 *latifolia* and 36 *murrayana* trees.

Explanations of statistical analyses procedures and a table of analyses of variance formats, with degrees of freedom indicated, are shown in table 1-2. In the results portion of this chapter standard deviations are noted in the text in parentheses following average values. Correlations of interest observed in *latifolia* between heartwood and sapwood characteristics and tree characteristics are also noted in the results section.

5-3 LITERATURE REVIEW

There is a considerable body of literature on heartwood and sapwood of lodgepole pine—much of it related to extractives, fungal attack, and to permeability and treatability. There is also a body of literature relating lodgepole pine sapwood amount to leaf area. These subjects are not within the scope of this paper, but for the benefit of readers wishing to study these subjects, following are pertinent references:

Extractives content and chemistry

Anderson and others (1969), Erdtman (1949), Harris (1969), Lieu and others (1979), Lindstedt (1949), Loman (1970a,1970b), Rickey and Hergert (1974), Shrimpton (1972,1973)

Fungi in sapwood

Ballard and others (1984)

Fungi in heartwood

Bourchier (1961a,1961b), Denyer (1952), Eades and Roff (1957,1959), Englerth and Scheffer (1955), Eslyn (1979), Loman (1970a,1970b), Loman and Paul (1963)

Permeability and treatability

Alexander (1934), Cooper (1973), Cooper and others (1974), Fosberg (1970), Graham (1956), Harris (1969), Lowery and Rasmussen (1965), Markstrom and others (1970), Markstrom and Hann (1972), Meyer (1974), Owston and others (1972), Ruddick (1980)

Sapwood amount related to leaf area

Kaufmann and Troendle (1981), Lopushinsky (1975), Pearson (1982), Running (1980), Thompson (1985), Waring and others (1982)

Following is a summary of the literature on heartwood-sapwood distribution within stems, moisture content, weight, and specific gravity.

Sapwood Thickness

Within-Tree Variation—From study of 19 *Pinus contorta* Dougl. ex Loud. from the east shore of Vancouver Island, Yang (1985) concluded that lodgepole pine sapwood thickness ranges from 20 to 30 mm for both north and south aspects, except at stump height (0.15 m above ground level), where it is 50 mm wide. He found that the number of growth rings in sapwood ranges from 25 to 50, and decreases from ground level upward into the tree crown. He also observed that the lineal width of sapwood is consistent at various positions along the tree trunk and is independent of tree age, tree diameter, radial growth rate of the sapwood, and the radial growth rate of the whole tree. The number of growth rings in sapwood, however, he found to be strongly correlated with tree age, tree diameter, radial growth rate of the sapwood, and the radial growth rate of the whole tree. Yang found no statistically significant relationship between sapwood width and number of sapwood growth rings.

At Breast Height—Lassen and Okkonen (1969) measured sapwood thickness at breast height on 3,290

lodgepole pines sampled throughout the species range in the United States; both *latifolia* and *murrayana* were included in the sample. They found a more or less linear relationship between sapwood thickness and tree diameter, with trees measuring 150 mm d.b.h. inside bark having a sapwood thickness of about 38 mm and those 530 mm in d.b.h. inside bark having twice this thickness of sapwood.

In interior British Columbia—including areas adjacent to the Yukon Territory—Sylvander and Smith (1973) measured sapwood thickness at breast height in 803 lodgepole pines averaging 254 mm d.b.h. and 67 years of age. They found that sapwood thickness averaged 45 mm or 18 percent of d.b.h., with standard deviation of 6.7 percentage points. Sapwood thickness increased with increasing d.b.h. and also with longitude; it was negatively correlated with tree age and also decreased at higher elevations and in the more northerly latitudes. They developed a regression equation including these five variables that accounted for 42 percent of the observed variation in sapwood thickness at breast height. Rapidly growing trees had wider sapwood than the slow growers.

Brazier (1980) studied lodgepole pine grown in Wales, England, and Scotland from coastal and interior North American provenances. When sampled 0.75 to 1.40 m from stump height, trees averaged 18 growth rings, and all trees contained heartwood. Width of sapwood varied with provenance (29 to 53 mm and 10 to 15 growth rings), but averaged 41 mm and 13 growth rings. Heartwood radius varied from 14 to 28 mm (3 to 10 growth rings) and averaged 17 mm (5 growth rings) in radius.

In Poles—Alexander (1934) studied 100 Class A, 7.6-m-long telephone poles with average top diameter of 203 mm—all cut in British Columbia and Alberta. From disks cut from butt, top, and an intermediate point, he found that sapwood thickness averaged 44 mm and that sapwood accounted for 53 percent of the cross-sectional area.

In a study of lodgepole pine 9.1-m-long Class 6 and 7 poles sampled near Libby, MT, Lowery and Rasmussen (1965) found that average sapwood thickness ranged from 11 to 38 mm and averaged 18 mm.

In Posts—From study of 107-mm-diameter posts averaging 1.6 annual rings/mm sampled near Fort Collins, CO, Markstrom and others (1970) found that sapwood thickness varied from 18 to 33 mm, with average of 25 mm.

Heartwood Proportion of Stem Volume

Hakkila and Panhelainen (1970) sampled lodgepole pine grown in northern (66.5 degrees latitude) and southern (60 to 62 degrees latitude) Finland from seed derived from Alberta and British Columbia sources; mean age of the trees was 40 years, d.b.h. averaged 128 mm, and height averaged 13.4 m. Average heartwood proportion of entire stemwood volume was 17.5 percent, with standard deviation of 9.1 percentage points. Of external tree characteristics, tree height best explained variation in percentage heartwood, as follows ($R^2 = 0.35$; standard error of the estimate = 7.31 percent):

$$Y = 4.50 + 0.0653X$$

where:

Y = heartwood percentage of entire stem volume

X = tree height, m.

Stands in the north of Finland did not differ significantly in heartwood content from those in the south. In southern stands, a three-component equation for prediction for heartwood content was developed, as follows ($R^2 = 0.75$; standard error of the estimate = 3.66 percent):

$$Y = -48.03 + 1.336X - 0.303CR + 0.145G$$

where:

X = tree height, m

CR = crown ratio

G = stemwood specific gravity, basis of green weight and oven-dry volume.

Hakkila and Panhelainen also found that the percentage of heartwood increases about 5 percentage points from stump height to a maximum at 10 to 20 percent of tree height, and then declines toward the crown. They concluded that heartwood volume percentage (Y) of stemwood volume was best estimated from a disk at 40 percent of tree height, as follows ($R^2 = 0.875$; standard error of the estimate = 3.4 percentage points):

$$Y = 3.03 + 0.874 \text{ (heartwood percentage at 40 percent of tree height)}$$

It can also be estimated from heartwood percentage at breast height ($R^2 = 0.841$; standard error of the estimate = 4.4 percentage points):

$$Y = 0.48 + 0.780 \text{ (heartwood percentage at breast height)}$$

In a sample of lodgepole pine grown in New Zealand from seed originally obtained from the northwestern part of the United States (*murrayana* as well as *latifolia*), Harris (1973) found that heartwood percentage of stemwood volume was positively correlated with stem volume, ranging from 18 percent to 41 percent, as follows:

Stem volume	Heartwood volume
m ³	Percent of stemwood volume
0.91	41
.91	23
.77	38
.62	32
.59	20
.46	29
.22	27
.19	18

Sapwood Area Related to Foliage Weight

Based on 12 lodgepole pines 10 to 60 years old destructively sampled in the Central Colorado Mountains at an elevation of 2,700 m, Running (1980) developed the follow-

ing equation for predicting foliage ovendry weight from sapwood basal area at breast height ($R^2 = 0.94$):

$$Y = -0.76 + 0.051X$$

where:

Y = foliage ovendry weight, kg

X = sapwood basal area, cm^2 .

Kaufmann and Troendle (1981) also found that ovendry foliage weight of lodgepole pine was linearly related to sapwood cross-sectional area at breast height in the stem, as follows ($R^2 = 0.95$):

$$\begin{aligned} \text{Dry foliage weight, g} = \\ 46.2 (\text{sapwood cross-sectional area, cm}^2) \end{aligned}$$

This equation is based on 11 trees sampled in August and September at about 915 m elevation near Fraser, CO.

Moisture Content

In British Columbia, Reid (1961) observed that the moisture content of *latifolia* sapwood normally averages in the range from 85 to 165 percent of ovendry weight; he found heartwood averaged about 30 percent moisture content. He also found that the moisture content of outer sapwood and inner bark was about 10 percentage points greater at 4 a.m. than from 4 to 8 p.m.; noontime moisture content was intermediate. His data indicated an outer sapwood moisture content of about 150 percent of ovendry weight, with inner sapwood having a much lower moisture content—about 50 percent. He noted that outer heartwood had about 25 percent moisture content and innermost heartwood about 40 percent (fig. 2-1).

Because snow prevented access to upper elevations from early November to early June, tree collections for the study here reported were made during the months of June through October in 1983 and 1984. Interpretation of data reported in the results section of this chapter should be tempered with knowledge that some variation in tree component moisture content occurs with both year and season sampled. For example, Markstrom and Hann (1972) found that in five trees sampled each season near Fort Collins, CO, sapwood of 156- to 242-year-old *latifolia* had higher moisture content in 1967 than in 1968, and that moisture content was least in spring and most in fall and winter, as follows:

Year and season	Sapwood		Heartwood	
	Outer	Inner	Outer	Inner
- - - - Percent of ovendry weight - - - -				
1967				
Spring growing	138	138	35	43
Summer	145	144	42	48
Fall dormancy	161	147	39	47
Winter	173	164	43	68
1968				
Spring growing	127	131	36	47
Summer	150	150	42	55

The foregoing data are based on increment cores removed at 0.91 and 1.22 m above ground level.

Weight

No data relating heartwood and sapwood weights to tree characteristics were found in the literature.

Specific Gravity

No data comparing the specific gravities of heartwood and sapwood were found in the literature, but Englerth and Scheffer (1955)—in a study of natural decay resistance of 10 lodgepole pines 9.4 to 14.3 inches in diameter and 58 to 220 years old—found that specific gravity of outer heartwood 4 to 6 feet above stump ranged from 0.42 to 0.57, with average of 0.48 (based on volume and weight when ovendry).

5-4 PROCEDURE

Procedural details of the experiment are given in chapter 1, and will not be repeated here except to note that the elevational zones of low, medium, and high are relative. Medium refers to an elevation that is medium for the variety at the latitude at which sampled; similarly, low and high refer to lower and upper elevational zones in which the variety occurs at the latitude sampled. *Latifolia* elevational zones were highest in the south (2,481, 2,711, and 3,144 m at 40 degrees) and progressively lower with each more northerly latitude (604, 739, and 879 m at 60 degrees). *Murrayana* was sampled at elevations in the range from 1,148 to 2,402 m.

Trees were uprooted (with central taproot intact and with lateral roots severed at a radius of 305 mm from tree pith) from level benches in natural unthinned stands within National or Provincial Forests. The sampling scheme resulted in selection of 76-, 152-, and 228-mm trees averaging 71, 91, and 107 years of age (at stump height of 152 mm), respectively, for *latifolia*, and 67, 84, and 91 years for *murrayana*. Most of the small-diameter trees were suppressed, while the larger trees were the fast growers.

At levels of 0, 10, 20, 30, 40, 50, 60, 70, 80, and 90 percent of tree height above a 152-mm-high stump, disks were removed in the field for laboratory analyses. In the laboratory, after determination of green diskwood volume and weight, heartwood was indicated by application of ferric chloride solution (10 g FeCl_3 in 90 g of water) and split away from the sapwood; average heartwood diameter was then measured and weight and volume of the green heartwood recorded. Ovendry weights of sapwood and heartwood were then determined and recorded. From these data stem-component specific gravities, weights, and volumes could be computed.

5-5 RESULTS—LATIFOLIA

In the following paragraphs summarizing results, only those main effects and interactions shown statistically significant (0.05 level) by analyses of variance are discussed, tabulated, and graphed. All reported correlations are statistically significant (0.05 level).

Stemwood average heartwood and sapwood characteristics are summarized in table 5-1. Variations of these characteristics with height in stems are summarized in table 5-2. Interpretation of these averages requires reference to the main effects and interactions related to

d.b.h., latitude, and elevational zone—as discussed in the remainder of this chapter.

None of the heartwood or sapwood characteristics studied were correlated with longitudinal zone; that is, with east-west location within a particular latitudinal sampling zone.

Table 5-1—Characteristics of heartwood and sapwood from *latifolia* and *murrayana* trees according to d.b.h. classes of 76, 152, and 228 mm¹

Statistic	<i>Latifolia</i>			<i>Murrayana</i>		
	76	152	228	76	152	228
Moisture content of entire stemwood component, percent of oven-dry weight						
Sapwood ²	110	122	126	104	128	142
Heartwood ²	47	42	41	47	44	43
Specific gravity, basis of green volume and oven-dry weight—entire component						
Sapwood ³	0.423	0.415	0.405	0.476	0.433	0.401
Heartwood ³	0.459	0.430	0.412	0.550	0.508	0.446
Heartwood percentage of stemwood volume	22.0	28.3	34.2	10.3	16.9	20.3
Heartwood percentage of stemwood weight						
Green-weight basis ³	18.4	21.6	25.7	8.8	12.9	14.3
Oven-dry-weight basis ³	22.6	28.8	34.6	11.4	18.3	21.5
Weight of sapwood in entire stem, ³ kg						
Green	14	91	226	14	89	254
Oven-dry	7	41	100	7	39	105
Weight of heartwood in entire stem, ³ kg						
Green	3.3	25.3	76.9	1.4	14.9	45.3
Oven-dry	2.3	17.9	54.3	1.0	10.5	32.2
Heartwood occurrence						
Age of lowest tree disk where heartwood does not occur, years	21	11	10	20	14	11
Height in tree at which heartwood no longer occurs, percent	76.1	89.5	93.6	60.8	80.0	88.3
Height in tree at which heartwood no longer occurs, m	7.2	14.0	17.9	4.7	11.3	16.6
Heartwood maximum diameter and location						
Heartwood maximum diameter, mm	36	85	147	27	67	108
Height of maximum diameter, percent	8.6	3.5	2.2	8.3	5.8	8.3
Height of this maximum diameter, m	0.80	0.53	0.44	0.60	0.78	1.33
At height of maximum heartwood diameter, heartwood percent stemwood diameter	48.2	53.8	59.9	36.3	44.1	48.0
Minimum sapwood thickness (where heartwood is present) and location						
Minimum thickness, mm	16	24	29	21	31	36
Height of this minimum, percent	51.3	60.5	70.5	43.3	54.2	77.5
Height of this minimum, m	4.8	9.3	13.3	3.2	7.4	14.6

¹Because of the main effects and interactions of d.b.h., latitude, and elevational zone, reference to appropriate figures and text discussion is required for interpretation of these data. Data are based on 243 *latifolia* trees (81 of each diameter), and 36 *murrayana* trees (12 of each diameter).

²From chapter 2.

³From chapter 4.

Table 5-2—Variations in heartwood and sapwood characteristics with height in stems of *latifolia* and *murrayana* trees of three diameters¹

Characteristic and d.b.h.	Height (percent)									
	0	10	20	30	40	50	60	70	80	90
<i>Latifolia</i>										
Heartwood diameter, mm										
76 mm	34	34	32	29	24	20	14	9	4	2
152 mm	83	79	74	66	58	48	38	25	15	4
228 mm	146	132	122	111	97	81	64	45	25	6
Sapwood thickness, mm										
76 mm	24	19	18	18	18	17	17	16	13	9
152 mm	40	31	30	29	30	30	29	28	25	17
228 mm	54	39	38	38	38	38	39	37	33	23
Heartwood percent of stemwood volume										
76 mm	22	28	27	24	22	19	13	10	4	1
152 mm	30	35	34	33	29	24	19	13	8	3
228 mm	37	42	40	38	34	30	25	19	12	5
Sapwood M.C. (percent) ²										
76 mm	103	101	104	108	112	117	122	126	129	121
152 mm	110	114	115	120	124	129	135	139	138	137
228 mm	117	118	122	125	130	136	139	142	142	135
Heartwood M.C. (percent) ²										
76 mm	46	46	47	48	48	51	50	52	55	53
152 mm	41	43	42	42	42	43	45	47	49	53
228 mm	40	42	42	41	42	41	42	44	46	50
Heartwood percent of stemwood, green weight										
76 mm	19	24	23	21	18	16	11	8	4	1
152 mm	24	27	27	25	22	18	14	10	6	2
228 mm	29	32	30	28	25	21	17	13	8	3
Heartwood percent of stemwood, oven-dry weight										
76 mm	23	28	28	25	22	19	15	10	5	1
152 mm	30	34	34	31	28	24	20	14	9	3
228 mm	37	41	39	37	34	30	25	19	12	4
Sapwood specific gravity ³										
76 mm	0.462	0.440	0.425	0.417	0.406	0.399	0.394	0.397	0.398	0.413
152 mm	.450	.426	.421	.412	.405	.398	.391	.385	.385	.393
228 mm	.435	.414	.406	.401	.395	.389	.384	.380	.382	.391
Heartwood specific gravity ³										
76 mm	.512	.462	.443	.432	.429	.430	.437	.450	.462	.454
152 mm	.482	.419	.414	.411	.416	.419	.423	.435	.451	.481
228 mm	.452	.404	.395	.395	.396	.403	.416	.421	.445	.480

(con.)

Table 5-2 (Con.)

Characteristic and d.b.h.	Height (percent)									
	0	10	20	30	40	50	60	70	80	90
<i>Murrayana</i>										
Heartwood diameter, mm										
76 mm	23	25	22	17	12	8	4	1	0	0
152 mm	64	62	55	45	36	28	20	11	4	0
228 mm	105	106	96	86	70	55	40	24	12	1
Sapwood thickness, mm										
76 mm	26	24	24	24	24	22	20	17	13	8
152 mm	50	40	39	39	39	37	35	31	26	15
228 mm	73	53	50	50	50	49	49	44	35	22
Heartwood percent of stemwood volume										
76 mm	13	15	14	11	7	5	3	1	0	0
152 mm	19	24	22	18	15	12	8	4	1	0
228 mm	20	28	26	24	19	15	11	6	4	1
Sapwood M.C. (percent) ²										
76 mm	93	99	103	106	106	112	120	121	123	119
152 mm	111	126	125	131	136	143	142	146	142	140
228 mm	133	140	144	138	148	153	150	154	157	139
Heartwood M.C. (percent) ²										
76 mm	46	45	50	47	47	53	57	50	40	—
152 mm	43	43	44	47	45	48	51	51	54	—
228 mm	45	42	41	42	43	43	44	49	52	46
Heartwood percent of stemwood, green weight										
76 mm	12	13	12	9	10	4	2	1	0	0
152 mm	16	18	17	14	11	8	6	3	1	0
228 mm	15	20	18	17	13	10	7	4	3	0
Heartwood percent of stemwood, oven-dry weight										
76 mm	14	17	15	12	8	5	3	1	0	0
152 mm	21	25	23	19	16	12	9	6	2	0
228 mm	22	29	26	24	20	16	12	7	4	1
Sapwood specific gravity ³										
76 mm	0.523	0.495	0.474	0.462	0.460	0.453	0.443	0.443	0.439	0.440
152 mm	.484	.442	.437	.423	.415	.401	.403	.397	.407	.404
228 mm	.431	.405	.394	.399	.386	.380	.385	.384	.383	.408
Heartwood specific gravity ³										
76 mm	.590	.571	.513	.532	.508	.508	.459	.558	.385	—
152 mm	.565	.499	.486	.458	.462	.455	.464	.470	.499	—
228 mm	.509	.443	.417	.424	.420	.442	.456	.458	.472	.502

¹Because of the main effects and interactions of d.b.h., latitude, and elevational zone, reference to the appropriate figures and text discussion is required for interpretation of these data. Data are based on 243 *latifolia* trees (81 of each diameter) and 36 *murrayana* trees (12 of each diameter).

²Percent of oven-dry weight.

³Based on oven-dry weight and green volume.

Heartwood Occurrence

Age of Lowest Tree Disk Where Heartwood Does Not Occur—The age of the lowest tree disk where heartwood did not occur averaged 14.20 years, with standard deviation of 11.43 years. It was unrelated to elevational zone, but was negatively correlated with d.b.h., averaging 20.87 (11.47 standard deviation), 11.49 (9.50), and 10.23 (10.24) years for trees 76, 152, and 228 mm in diameter (fig. 5-1). This age was also negatively correlated with latitude; for example, it averaged 27 years at 40 degrees latitude and only 8 years at 57.5 degrees (fig. 5-1).

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the age of the lowest tree disk where heartwood does not occur with other tree statistics are of interest:

Statistic	<i>r</i>
Percentage of stem height where heartwood no longer occurs	−0.531
Height (m) where heartwood no longer occurs	−.515
Height (m) where sapwood thickness is minimum	−.455
Heartwood maximum diameter	−.442
Green weight of heartwood	−.423
Ovendry weight of heartwood	−.418
Tree height	.403
Elevation	.394
D.b.h.	−.384
Heartwood volume as percentage of bark-free stem volume	−.370
Heartwood as percentage of bark-free ovendry stem weight	−.364
Ovendry weight of stump-root system (wood plus bark)	−.364
Ovendry weight of stem (wood plus bark)	−.356
Stemwood d.i.b. (diameter inside bark) at base of live crown	−.345
Heartwood as percentage of bark-free stem weight, green	−.344
Percentage of stem height where sapwood is thinnest	−.321
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	−.307
Average branch diameter	−.304

In the foregoing tabulation, 16 of the 18 are negative correlations. The two positive correlations suggest that age of the lowest tree disk free of heartwood is greatest in tall trees growing at high elevation. The negative correlations suggest that this age tends to be greatest in trees in which heartwood does not extend far up the tree, sapwood has minimum thickness low in the tree, heartwood maximum diameter is small, weight of heartwood is small, d.b.h. is small, heartwood weight and volume as percentage of stemwood is small, stump-root weight is small, and stemwood d.i.b. at the base of the live crown is small.

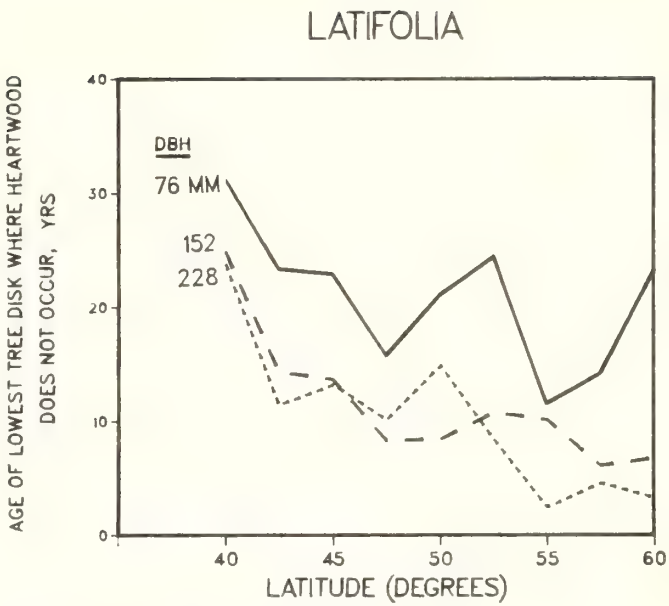


Figure 5-1—Age of lowest tree disk where heartwood does not occur in *latifolia* trees of three diameters, related to latitude.

Height in the Tree at Which Heartwood No Longer Occurs, Percent—Percentage height in the tree above which heartwood did not occur averaged 86.38 percent, with standard deviation of 14.86 percent. This percentage was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 76.05 (18.82), 89.51 (9.99), and 93.58 (6.58) for trees of the three diameter classes (fig. 5-2). It also was positively correlated with latitude; for example, the percentage averaged 79 percent at 40 degrees and 96 percent at 60 degrees (fig. 5-2).

The following significant correlations (arbitrarily truncated at $r = 0.500$) of the percentage height in the tree at which heartwood no longer occurred with other tree statistics are of interest:

Statistic	<i>r</i>
Heartwood as percentage of stemwood diameter at height of maximum heartwood diameter	0.777
Heartwood volume as percentage of entire stemwood volume	.734
Heartwood percentage of entire stemwood weight, ovendry	.730
Height in tree at which heartwood no longer occurs, m	.720
Heartwood percentage of entire stemwood weight, green	.681
Foliage percentage of complete-tree weight, ovendry	-.661
Heartwood maximum diameter	.644
Percentage moisture content of complete tree with foliage and cones	-.613
Percentage moisture content of complete tree without foliage and cones	-.610
Percentage moisture content of stem, wood plus bark	-.599
Percentage moisture content of complete tree, wood only	-.586
Percentage moisture content of stemwood, tree average	-.577
Percentage moisture content of stump-root system, wood plus bark	-.571
Percentage moisture content of wood of the stump-root system	-.567
Moisture content of stembark, tree average	-.559
Height in tree where minimum sapwood thickness occurs	.546
Tree height	.543
Within-crown stemwood as percentage of stemwood volume	-.541
Stembark specific gravity	.538
Tree age at 152-mm stump height	.532
Percentage moisture content of complete-tree bark	-.531
Age of lowest tree disk where heartwood does not occur	-.531
Green weight of heartwood of entire stem	.518
Ovendry weight of heartwood of entire stem	.518
Crown ratio	-.501

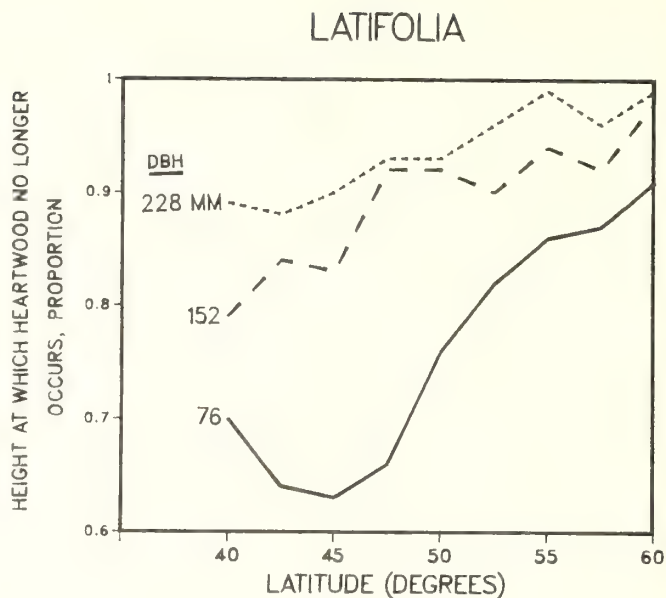


Figure 5-2—Height in tree (proportion) at which heartwood does not occur in *latifolia* trees of three diameters, related to latitude.

These correlation coefficients suggest that heartwood extends upward the greatest percentage of tree height in taller and older trees in which maximum heartwood diameter (as a percentage of tree diameter) is large, heartwood weight and volume (as percentages of stemwood weight and volume) are large, foliage ovendry weight (as a percentage of complete-tree weight) is small, percentage moisture content of complete tree and stem and root are low, minimum sapwood thickness occurs high in the stem, within-crown stemwood percentage of total stemwood volume is low, stembark specific gravity is high and moisture content low, age of the lowest disk in which heartwood does not occur is low, and crown ratio is low.

Height in the Tree at Which Heartwood No Longer Occurs, Meters—The height (meters) in the trees at which heartwood no longer occurred was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 7.19 (2.65), 14.00 (3.10), and 17.87 (3.12) m for trees of the three diameter classes (fig. 5-3). This height was also positively correlated with latitude; for example, it averaged 10.9 m at 40 degrees and 15.4 m at 55 degrees latitude (fig. 5-3).

The following significant correlations (arbitrarily truncated at $r = 0.50$) of height in tree (meters) at which heartwood no longer occurs, with other tree statistics are of interest:

Statistic	<i>r</i>
Tree height	0.966
Ovendry weight of stem, wood plus bark	.876
Heartwood maximum diameter	.838
D.b.h.	.821
Ovendry weight of entire heartwood	.815
Ovendry weight of stump-root system, wood plus bark	.811
Green weight of entire heartwood	.809
Ovendry weight of entire sapwood	.808
Green weight of entire sapwood	.770
Height in tree at which heartwood no longer occurs, percent	.720
Height in tree where minimum sapwood thickness occurs, m	.664
Stump-root system percentage of ovendry complete-tree weight	-.658
Stemwood d.i.b. at base of live crown	.637
Average branch diameter	.605
Foliage as percentage of ovendry weight of complete tree	-.588
Percentage moisture content of bark of complete tree	-.575
Weight of ovendry foliage	.565
Weight of ovendry branches, wood plus bark	.559
Number of live branches	.556
Stem (wood plus bark) as percentage of ovendry weight of complete tree	.556
Percentage moisture content of entire heartwood	-.544
Heartwood as percentage of stemwood diameter at height of maximum heartwood diameter	.543
Heartwood as percentage of stemwood volume	.541
Taproot length	.526
Percentage moisture content of complete-tree bark	-.526
Heartwood as percentage of ovendry stemwood weight	.517
Age of lowest stem disk above which heartwood does not occur	-.515

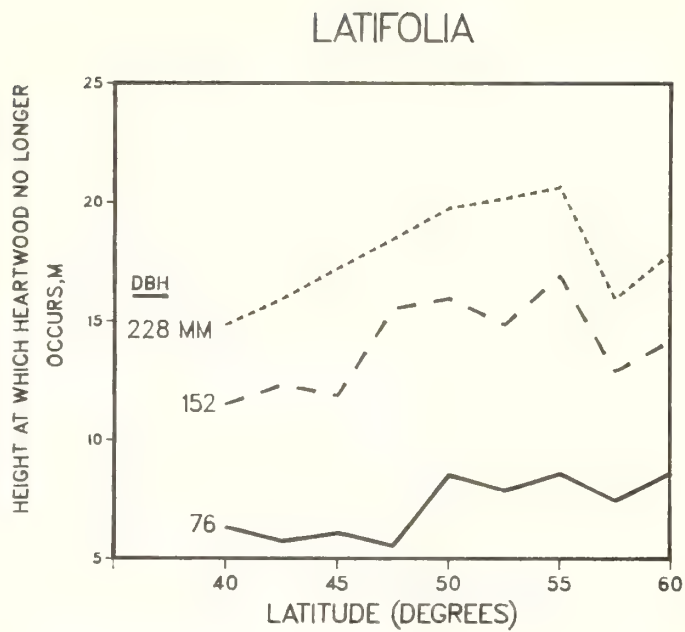


Figure 5-3—Height in tree (meters) at which heartwood does not occur in *latifolia* trees, related to latitude.

These data suggest that heartwood extends upward in stems the greatest distance (meters) in large-diameter, tall trees, with numerous large, heavy branches, heavy foliage, and heavy stems comprising a high percentage of complete-tree weight, and in which heartwood diameter and weight are large, stump-root weight is large (but stump-root percentage of complete-tree weight is small), sapwood weight is large, minimum sapwood thickness occurs high in the tree, stemwood d.i.b. at the base of the live crown is large, foliage as percentage of ovendry weight of complete tree is small, percentage moisture content of complete-tree bark and of heartwood are both low, heartwood as percentage of stemwood diameter and volume are high, taproots are long, and age of lowest stem disk above which heartwood does not occur is low.

Heartwood Maximum Diameter and Location

Heartwood Maximum Diameter—Heartwood maximum diameter was unrelated to elevational zone but was positively correlated to d.b.h., averaging 36.1 (15.1), 85.3 (25.6), and 146.9 (32.2) mm for trees of the three diameter classes (fig. 5-4). It was also positively correlated with latitude; with diameter data pooled, maximum heartwood diameter averaged 71 mm at 42.5 degrees and 104 mm at 60 degrees (fig. 5-4).

The following significant correlations (arbitrarily truncated at $r = 0.500$) of heartwood maximum diameter with other tree statistics are of interest:

Statistic	<i>r</i>
Ovendry weight of entire heartwood	0.913
Green weight of entire heartwood	.911
D.b.h.	.875
Ovendry weight of stump-root system, wood plus bark	.873
Ovendry weight of stem, wood plus bark	.869
Height in tree (m) above which heartwood does not occur	.838
Tree height	.782
Average branch diameter	.766
Ovendry weight of entire sapwood	.730
Stemwood d.i.b. at base of live crown	.697
Green weight of sapwood	.690
Heartwood as percentage of volume of stemwood	.681
Ovendry weight of live branches	.676
Heartwood as percentage of oven-dry weight of stemwood	.673
Heartwood as percentage of stemwood diameter at height of maximum heartwood diameter	.651
Percentage height in tree above which heartwood does not occur	.644
Ovendry foliage weight	.631
Percentage moisture content of stembark, tree average	-.603
Heartwood as percentage of green stemwood weight	.600
Within-crown stemwood taper, mm/m	.587
Number of cones on the tip 305 mm of the top 25 branches	.572
Percentage moisture content of complete-tree bark	-.539
Height in tree where minimum sapwood thickness occurs, m	.534
Tree age at 152-mm stump height	.528
Ovendry weight of dead branches	.523
Stump-root system (wood plus bark) as percentage of oven-dry weight of complete tree	-.500

LATIFOLIA

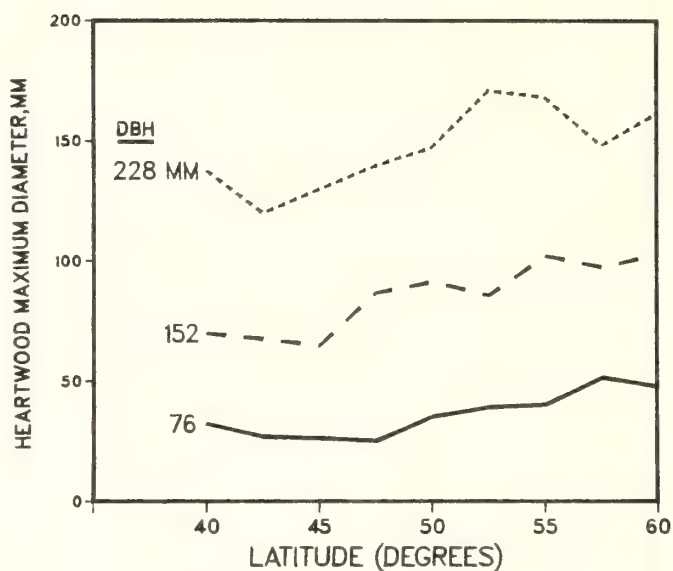


Figure 5-4—Heartwood maximum diameter in *latifolia* trees of three diameters, related to latitude.

These data suggest that largest heartwood diameter is found in large-diameter tall, old trees with large-diameter branches, many cones on the top 25 branches, large within-crown stem taper, heavy foliage, and a large oven-dry weight of dead branches. In addition to the obvious correlations with heartwood volume and weight, largest heartwood diameter tends to occur in trees with heavy stump-root systems (but comprising a low percentage of complete-tree weight), large stemwood d.i.b. at base of live crown, heavy crowns, and stembark and treebark of low percentage moisture content.

Height at Which Maximum Heartwood Diameter Occurs, Percent—The percentage of tree height at which maximum heartwood diameter occurred was generally not far above stump height, but this percentage was negatively correlated with d.b.h., averaging 8.64 (8.02), 3.46 (5.95), and 2.22 (4.18) percent for trees 76, 152, and 228 mm in d.b.h. The percentage height at which the maximum occurred was generally also negatively correlated with latitude (averaging 7.4 percent at 40 degrees and 1.5 percent at 57.5 degrees), but interactions of latitude, elevational zone, and d.b.h. were complex (fig. 5-5).

The following significant correlations (arbitrarily truncated at $r = 0.250$) of the percentage of total height in trees at which maximum heartwood diameter occurred with other tree statistics are of interest:

Statistic	<i>r</i>
Height in trees (m) of maximum heartwood diameter	0.906
Heartwood maximum diameter	-.481
D.b.h.	-.387
Ovendry weight of entire heartwood	-.379
Green weight of entire heartwood	-.379
Ovendry weight of stump-root system, wood plus bark	-.362
Height in tree (m) above which heartwood does not occur	-.359
Heartwood as percentage of volume of entire stemwood	-.358
Heartwood as percentage of weight, oven-dry, of entire stemwood	-.352
Tree height	-.340
Ovendry stem weight, wood plus bark	-.339
Heartwood as percentage of weight, green, of entire stemwood	-.327
Average branch diameter	-.318
Stemwood d.i.b. at base of live crown	-.297
Percentage moisture content of stump-root system, wood plus bark	.293
Age of the lowest stem disk in which heartwood does not occur	.292
Ovendry weight of live branches, wood plus bark	-.286
Ovendry foliage weight	-.285
Percentage moisture content of entire stembark	.284
Percentage moisture content of bark of stump-root system	.277
Below-crown stemwood taper, mm/m	-.274
Bark thickness at 152-mm stump height	-.272
Percentage moisture content of wood of stump-root system	.270
Ovendry weight of entire sapwood	-.268
Percentage moisture content of bark of complete tree	.268
Percentage moisture content of complete tree with foliage and cones	.259
Percentage moisture content of complete tree without foliage or cones	.257
Percentage height in tree above which heartwood does not occur	-.253

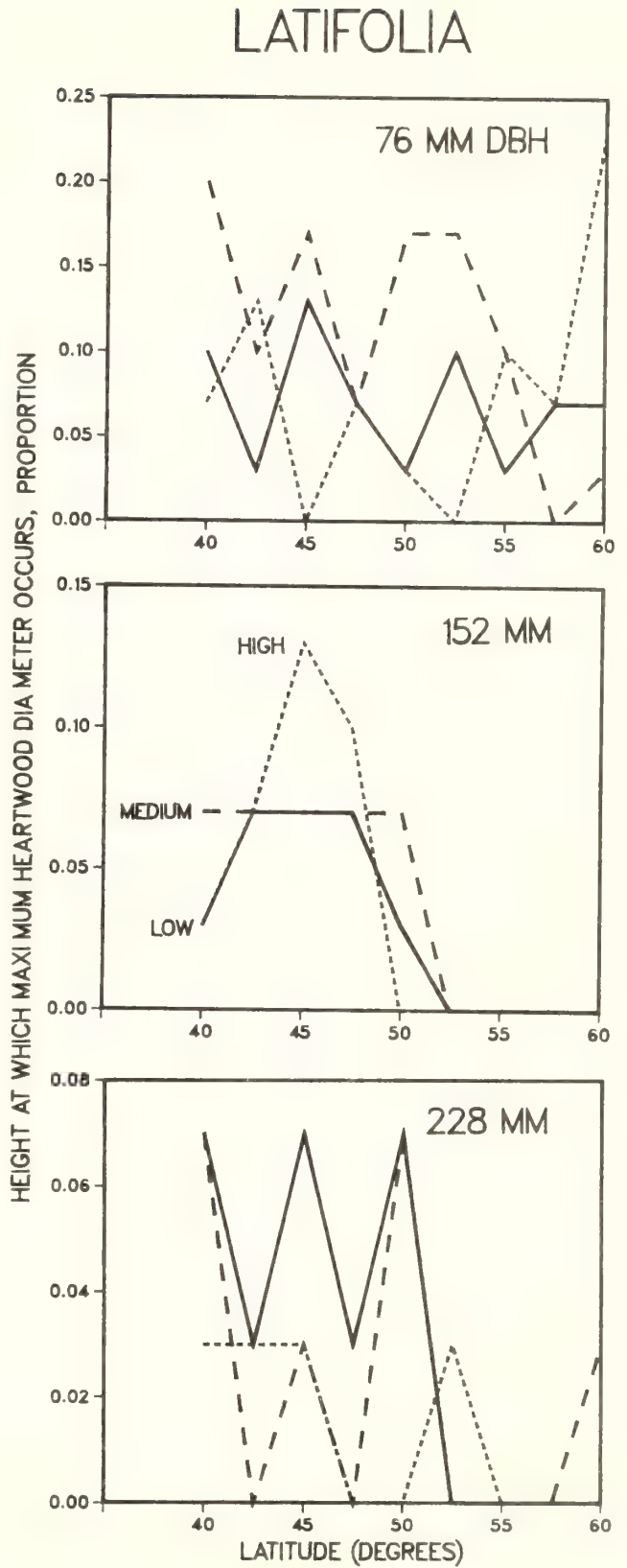


Figure 5-5—Proportion of height at which maximum heartwood diameter occurs in *latifolia* trees of three diameters, related to latitude and elevational zone.

These data suggest that maximum heartwood diameter occurs at greatest percentage of tree height in small-diameter, short, light-weight trees with small branches, and low weight of branches, foliage, and stump-root systems.

Of the 28 characteristics listed in the foregoing tabulation, only nine are positively correlated. Thus, maximum heartwood diameter occurs at greatest percentage of tree height in trees in which percentage moisture content of the stump-root system is high, percentage moisture content of stembark and treebark is high, percentage moisture content of the complete tree is high, and the age of the lowest tree disk in which heartwood does not occur is high.

The negative correlations further indicate that maximum heartwood diameter occurs at the greatest percentage of tree height in trees in which maximum heartwood diameter is small, heartwood weight is small, heartwood comprises a small percentage of stemwood weight, stemwood d.i.b. at the base of the live crown is small, below-crown stemwood taper is small, bark at stump height is thin, sapwood weight is small, and percentage of tree height above which heartwood does not occur is small.

Height at Which Maximum Heartwood Diameter Occurs, Meters—The height (meters) at which maximum heartwood diameter occurred was unrelated to elevational zone but was negatively correlated with d.b.h., averaging 0.80 (0.74), 0.53 (0.92), and 0.44 (0.84) m for trees 76, 152,

and 228 mm in d.b.h. This height was generally negatively correlated with latitude—averaging 0.89 m at 40 degrees and only 0.13 m at 57.5 degrees, but the relationship varied with d.b.h. (fig. 5-6).

The following significant correlations (arbitrarily truncated at $r = 0.200$) of the height (meters) at which maximum heartwood diameter occurred with other tree statistics are of interest:

Statistic	<i>r</i>
Height (percent) where maximum heartwood diameter occurs	0.906
Heartwood maximum diameter	-.338
Heartwood as percentage of weight of bark-free stem, ovendry	-.325
Heartwood as percentage of stemwood volume	-.323
Heartwood as percentage of weight of bark-free stem, green	-.317
Percentage moisture content of stump-root system (wood plus bark)	.272
Percentage moisture content of wood of stump-root system	.258
Green weight of heartwood	-.257
Ovendry weight of heartwood	-.255
Percentage moisture content of complete tree with foliage and cones	.251
Percentage moisture content of complete tree without foliage or cones	.250
Percentage moisture content of complete tree (wood only)	.240
Percentage moisture content of stem (wood plus bark)	.237
Below-crown average stemwood taper, mm/m	-.233
Percentage moisture content of stemwood, tree average	.224
Within-crown stemwood taper, mm/m	-.215
Age of the lowest tree disk in which heartwood does not occur	.207
Elevation, m	.206

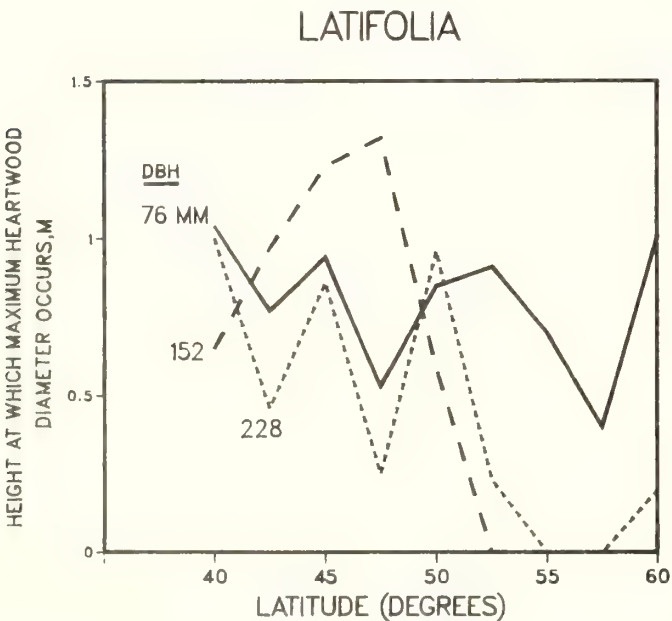


Figure 5-6—Height (meters) at which maximum heartwood diameter occurs in *latifolia* trees of three diameters, related to latitude.

The foregoing data suggest that the height (meters) at which maximum heartwood diameter occurs is greatest in trees growing at high elevation with high moisture content, little stem taper, and low heartwood content—and in those trees in which the age of the lowest tree disk in which heartwood does not occur is large.

Heartwood as Percentage of Stem Diameter, at Height of Maximum Heartwood Diameter—Heartwood as percentage of stem diameter at height of maximum heartwood diameter was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 48.15 (19.14), 53.80 (14.47), and 59.94 (11.36) percent for the three diameter classes. Differences between diameter classes were most pronounced at 40 to 50 degrees of latitude; also, heartwood as percentage of diameter was positively correlated with latitude, averaging minimum (43.13 percent) at 42.5 degrees and maximum (64.64 percent) at 60 degrees (fig. 5-7).

The following significant correlations (arbitrarily truncated at $r = 0.450$) of heartwood as percentage of stem diameter at height of maximum heartwood diameter with other tree statistics are of interest:

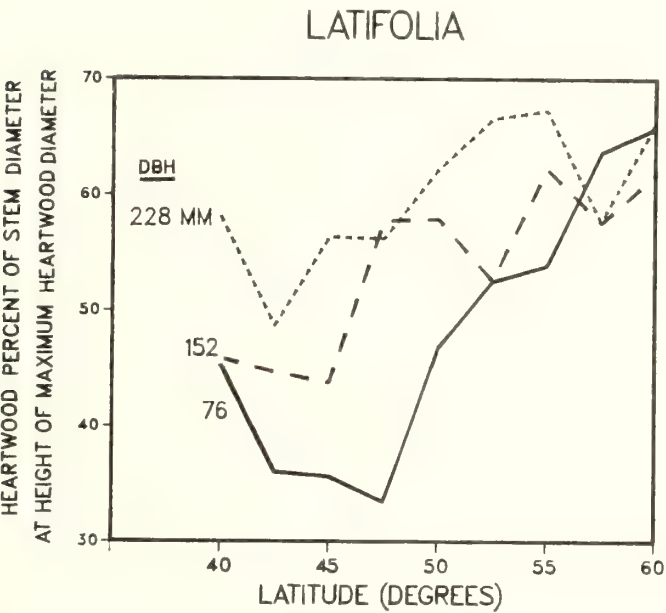


Figure 5-7—Heartwood as percentage of stem diameter at height of maximum heartwood diameter in *latifolia* trees of three diameters, related to latitude.

Statistic	r
Heartwood as percentage of stemwood volume	0.941
Heartwood as percentage of stemwood weight, ovendry	.937
Heartwood as percentage of stemwood weight, green	.917
Height (percent) of lowest tree disk in which heartwood does not occur	.777
Percentage moisture content of complete tree with foliage and cones	-.773
Percentage moisture content of complete tree without foliage or cones	-.763
Percentage moisture content of complete tree, wood only	-.754
Percentage moisture content of stem, wood plus bark	-.753
Percentage moisture content of stemwood, tree average	-.741
Foliage as percentage of complete-tree weight, ovendry	-.687
Percentage moisture content of wood of stump-root system	-.685
Percentage moisture content of stump-root system, wood plus bark	-.677
Heartwood maximum diameter	.651
Percentage moisture content of complete tree, bark only	-.590
Percentage moisture content of stembark, tree average	-.588
Within-crown stemwood percentage of entire stemwood volume	-.585
Stembark specific gravity	.583
Green weight of heartwood	.561
Ovendry weight of heartwood	.558
Crown ratio	-.545
Height (m) of lowest tree disk in which heartwood does not occur	.543
Percentage moisture content of foliage-free branches, wood plus bark	-.541
Stem (wood plus bark) as percentage of complete-tree weight, ovendry	.534
Tree age at 152-mm stump height	.486
Percentage moisture content of sapwood	-.474
Minimum sapwood thickness	-.452

The foregoing tabulation suggests that heartwood percentage of stemwood diameter at height of maximum heartwood diameter is maximum in older trees with low moisture content, low crown ratio, and with foliage comprising a low percentage of complete-tree weight. It also tends to be maximum in trees with high stembark specific gravity, a low percentage of within-crown stemwood, and—obviously—a high weight and volume content of heartwood and thin sapwood.

Heartwood Diameter by Level

Heartwood diameters at various proportions of tree height are positively correlated with d.b.h. (table 5-2 and figs. 5-8 and 5-9). They are also positively correlated with latitude (fig. 5-10).

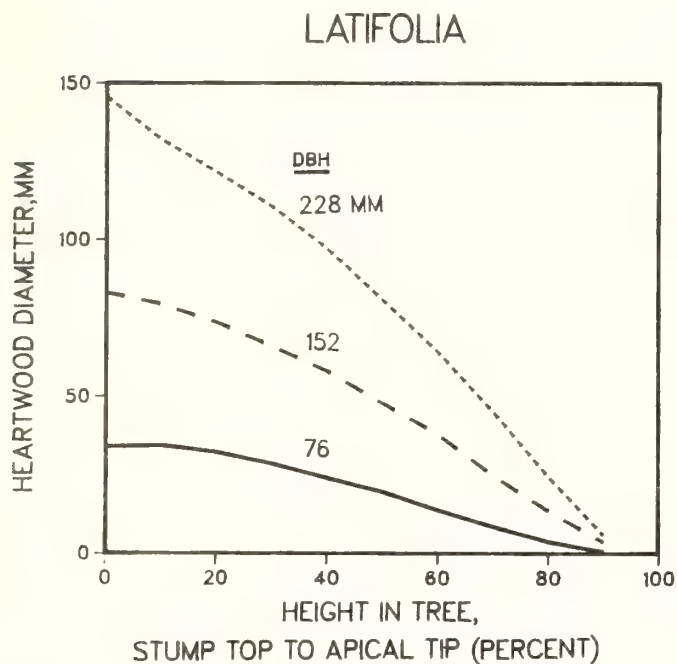


Figure 5-8—Heartwood diameter in *latifolia* trees of three diameters, related to height in tree.

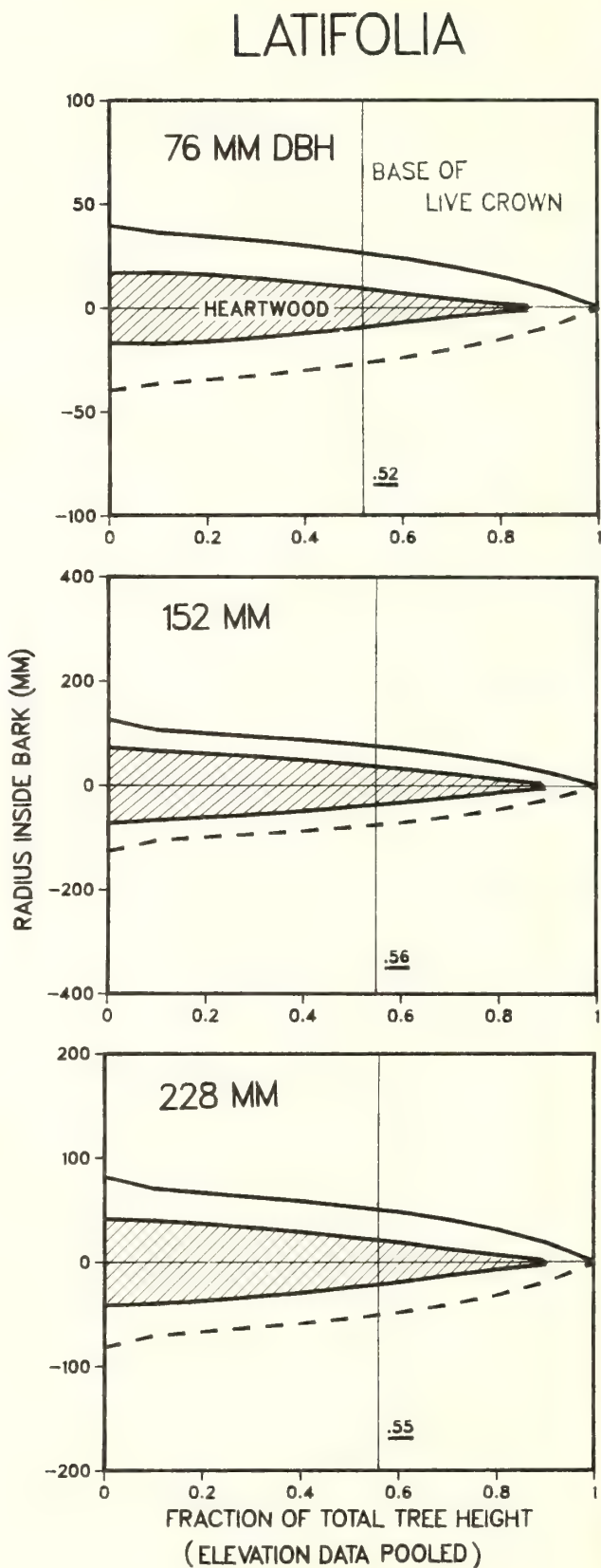


Figure 5-9—Heartwood and stemwood radius in *latifolia* trees of three diameters, related to height in tree and base of live crown.

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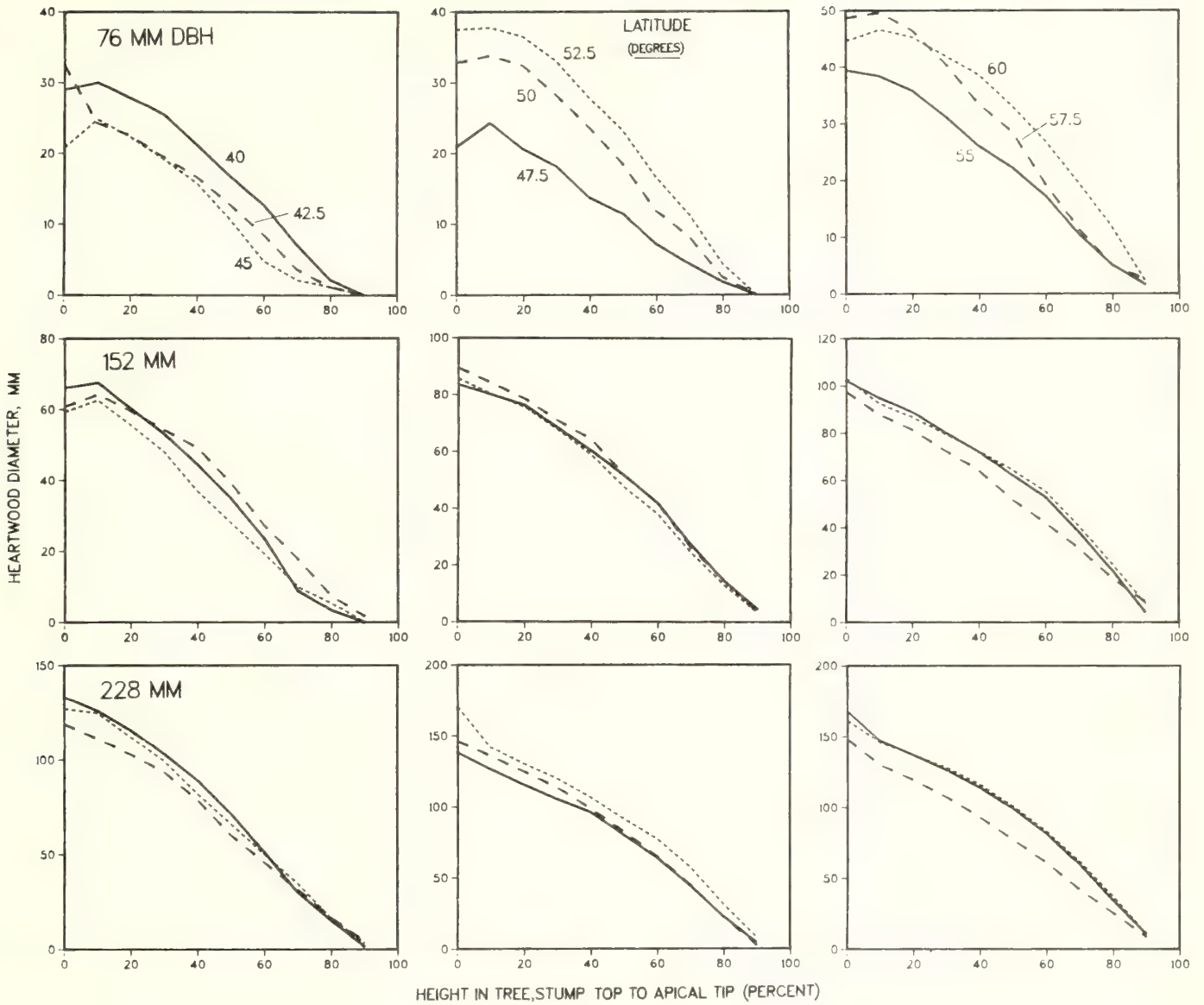


Figure 5-10—Heartwood diameter in *latifolia* trees of three diameters, related to height in tree and latitude.

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Minimum Sapwood Thickness and Location Where Heartwood Is Present

Minimum Thickness—Minimum sapwood thickness was positively correlated with d.b.h., averaging 16.03 (6.85), 23.81 (8.43), and 28.80 (8.76) mm for trees of the three diameter classes. It was negatively correlated with latitude; that is, trees in northern latitudes had thinner sapwood than those in the south (fig. 5-11). Minimum sapwood thickness was also significantly related to elevational zone; for all three d.b.h. classes, sapwood averaged thickest in trees from low-elevation zones; that is, 24.94, 21.64, and 22.06 mm for low-, medium-, and high-elevation zones (fig. 5-11).

Because woods with thin sapwood are difficult to treat with preservatives, significant correlations of minimum sapwood thickness (where heartwood is present) with other tree statistics are listed in considerable detail, as follows (list arbitrarily truncated at $r = 0.300$):

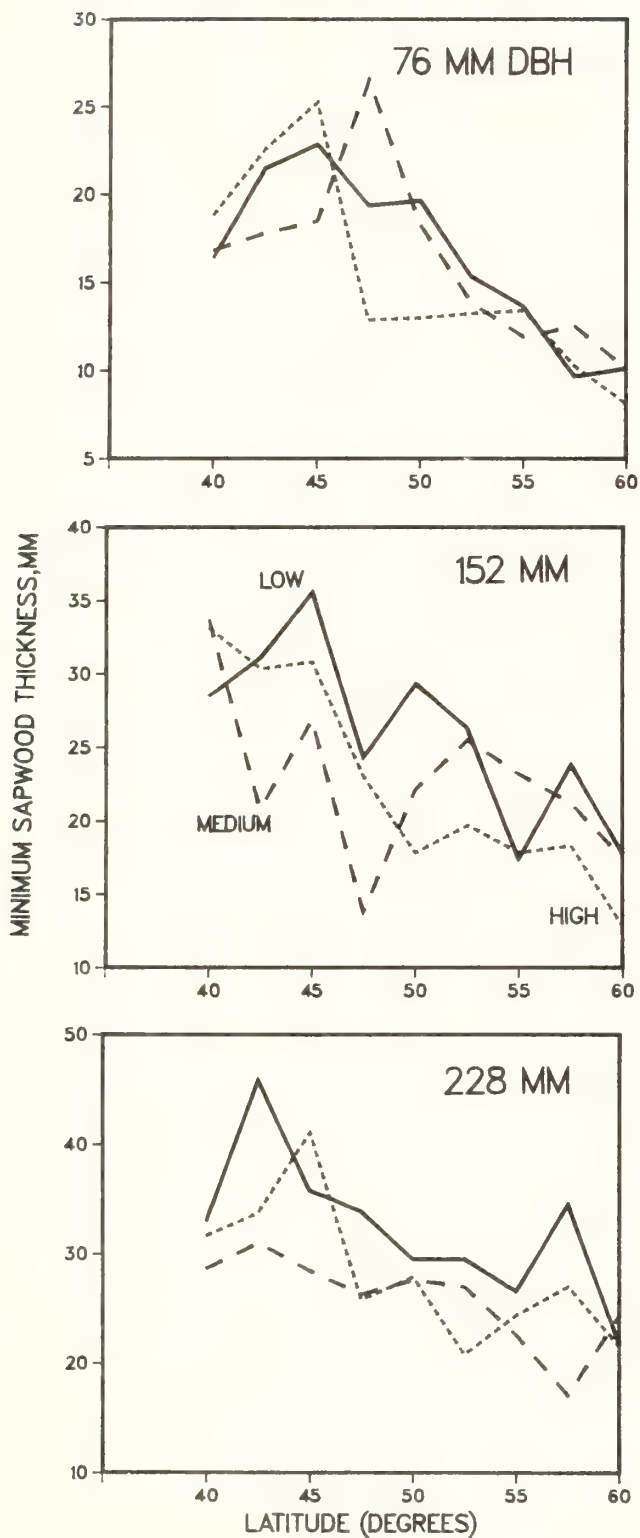


Figure 5-11—Minimum sapwood thickness in *latifolia* trees of three diameters, related to latitude and elevational zone.

Statistic	r
Average growth-ring width at 152-mm stump height	0.680
Green weight of sapwood	.652
Ovendry weight of sapwood	.618
Stemwood d.i.b. at base of live crown	.618
Number of live branches	.588
Ovendry foliage weight	.564
D.b.h.	.543
Heartwood as percentage of weight of bark-free stem, green	-.541
Percentage moisture content of sapwood	.533
Percentage moisture content of complete tree, wood only	.533
Percentage moisture content of stemwood, tree average	.524
Taproot length	.521
Percentage moisture content of complete tree without foliage or cones	.495
Percentage moisture content of stem, wood plus bark	.494
Ovendry weight of stump-root system, wood plus bark	.492
Heartwood as percentage of weight of bark-free stem, ovendry	-.488
Percentage moisture content of complete tree with foliage and cones	.481
Heartwood as percentage of stemwood volume	-.479
Ovendry weight of live branches, wood plus bark	.471
Percentage moisture content of foliage-free live branches, wood plus bark	.468
Ovendry weight of stem, wood plus bark	.459
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	-.452
Percentage moisture content of live branchwood	.443

(con.)

Statistic	<i>r</i>
Stemwood specific gravity	-.427
Tree height	.407
Live branch (wood plus bark) as percentage of complete-tree weight, ovendry	.396
Percentage moisture content of stump-root system	.394
Average branch angle	-.389
Average branch diameter	.362
Bark thickness at 152-mm stump height	.356
Percentage moisture content of stump-root system, wood plus bark	.354
Specific gravity of entire sapwood	-.350
Ovendry weight of dead branches	.321
Crown ratio	.315
Specific gravity of entire heartwood	-.313
Within-crown stemwood as percentage of entire stemwood volume	.313
Below-crown average stemwood taper, mm/m	.312
Elevation, m	.309
Percentage moisture content of live branchbark	.308

The foregoing tabulation suggests that sapwood tends to be thinnest in slow-grown, small-diameter, short, light-weight trees having a low crown ratio, little foliage, few branches of small diameter and low weight with large branch angles, and a lightweight stump-root system with short taproot.

Sapwood also tends to be thinnest in trees with thin bark at stump height, low moisture content in most components, little below-crown stemwood taper, and a small percentage of total stemwood volume within the crown.

Height at Which Minimum Sapwood Thickness Occurs, Percent—The percentage of tree height at which sapwood is thinnest was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 51.36 (25.19), 60.49 (28.50), and 70.49 (25.73) percent of tree height for the three diameter classes. Also, this percentage of height tended to increase with increasing latitude; for example, it averaged smallest (52.59 percent) at 45 degrees and largest (75.56 percent) at 60 degrees, but the relationship varied with diameter (fig. 5-12).

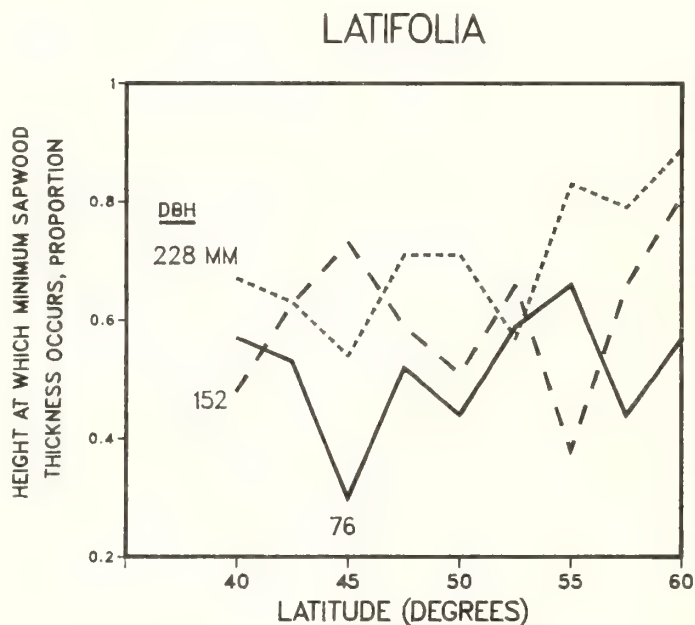


Figure 5-12—Proportion of tree height at which minimum sapwood thickness occurs in *latifolia* trees of three diameters, related to latitude.

The following significant correlations (arbitrarily truncated at $r = 0.200$) of the height of minimum sapwood thickness—where heartwood is present—expressed as percentage of tree height, with other tree statistics are of interest:

Statistic	<i>r</i>
Height in tree (m) where sapwood thickness is minimum	0.846
Height (percent) of lowest tree disk in which heartwood does not occur	.460
Ovendry foliage weight	.334
Age of the lowest tree disk in which heartwood does not occur	-.321
Stemwood d.i.b. at base of live crown	.308
Ovendry weight of live branches, wood plus bark	.297
D.b.h.	.287
Ovendry weight of stump-root system, wood plus bark	.276
Height (m) of lowest tree disk in which heartwood does not occur	.273
Average branch diameter	.257
Green weight of sapwood	.244
Bark thickness at 152-mm stump height	.242
Ovendry weight of sapwood	.239
Percentage moisture content of heartwood	-.225
Ovendry weight of stem, wood plus bark	.220
Heartwood maximum diameter	.220
Tree age at 152-mm stump height	.203

The foregoing tabulation suggests that the minimum sapwood thickness occurs at the highest percentage of tree height in older and larger trees having heavy stems and foliage, heavy stump-root systems, large-diameter branches, thick bark at stump height, and heavy sapwood content.

Also, percentage of tree height where minimum sapwood thickness occurs tends to be maximum in trees in which heartwood extends high in the stem, and in which heartwood has large maximum diameter and low moisture content.

Height at Which Minimum Sapwood Thickness Occurs, Meters—The height (meters) at which minimum sapwood thickness occurred (where heartwood was present) was unrelated to elevational zone or to latitude. It was, however, positively correlated to d.b.h., as follows:

D.b.h.	Height	Standard deviation
<i>mm</i>	<i>----- Meters -----</i>	
76	4.80	2.68
152	9.25	4.59
228	13.27	5.14

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the height (meters) at which minimum sapwood thickness occurs with other tree statistics are of interest:

Statistic	<i>r</i>
Height in tree (percent) where minimum sapwood thickness occurs	0.846
Height (m) of lowest tree disk in which heartwood does not occur	.664
D.b.h.	.633
Ovendry weight of sapwood	.622
Ovendry weight of stump-root system, wood plus bark	.621
Ovendry weight of stem, wood plus bark	.614
Green weight of sapwood	.613
Tree height	.606
Stemwood d.i.b. at base of live crown	.579
Ovendry foliage weight	.567
Height (percent) of lowest tree disk in which heartwood does not occur	.546
Heartwood maximum diameter	.534
Ovendry weight of live branches, wood plus bark	.522
Ovendry weight of heartwood	.476
Average branch diameter	.473
Green weight of heartwood	.468
Number of live branches	.464
Age of lowest tree disk in which heartwood does not occur	-.455
Bark thickness at 152-mm stump height	.440
Stump-root system (wood plus bark) as percentage of complete-tree weight, ovendry	-.415
Percentage moisture content of heartwood	-.392
Specific gravity of entire heartwood	-.367
Taproot length	.338
Number of cones on tip 305 mm of top 25 branches	.325
Percentage moisture content of stembark, tree average	-.313
Tree age at 152-mm stump height	.302

The foregoing tabulation suggests that the height (meters) of minimum sapwood thickness is highest in large-diameter, tall trees with heavy stems and foliage, heavy stump-root systems with long taproots (but comprising a small percentage of complete-tree weight), numerous large and heavy branches bearing numerous cones, large stemwood diameter at the base of the live crown, and thick bark at stump height.

Also, this height is greatest in trees having heartwood that extends high up in the stem, and which have low moisture content, low specific gravity, and large maximum diameter.

Sapwood Thickness by Level

Sapwood thickness is maximum near ground level, diminishes rapidly up to about 10 percent of tree height, then remains more or less constant up to about 70 percent of tree height, and finally diminishes with approach to the apical tip (fig. 5-13).

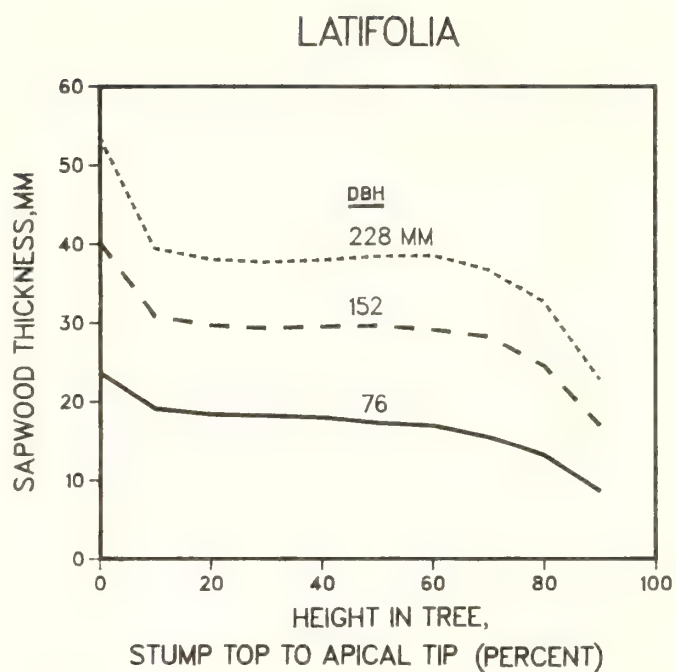


Figure 5-13—Sapwood thickness in *latifolia* trees of three diameters, related to height in tree.

It was unrelated to elevational zone, but positively correlated with d.b.h., averaging—at 40 percent of tree height—17.98 (6.11), 29.59 (9.94), and 38.00 (10.91) mm for trees of the three diameter classes (fig. 5-13). Sapwood was thickest in the three southernmost latitudes (32 to 36 mm at 40 percent of tree height), and thinnest in northern latitudes (21 mm at 40 percent of tree height at 60 degrees latitude); see figure 5-14.

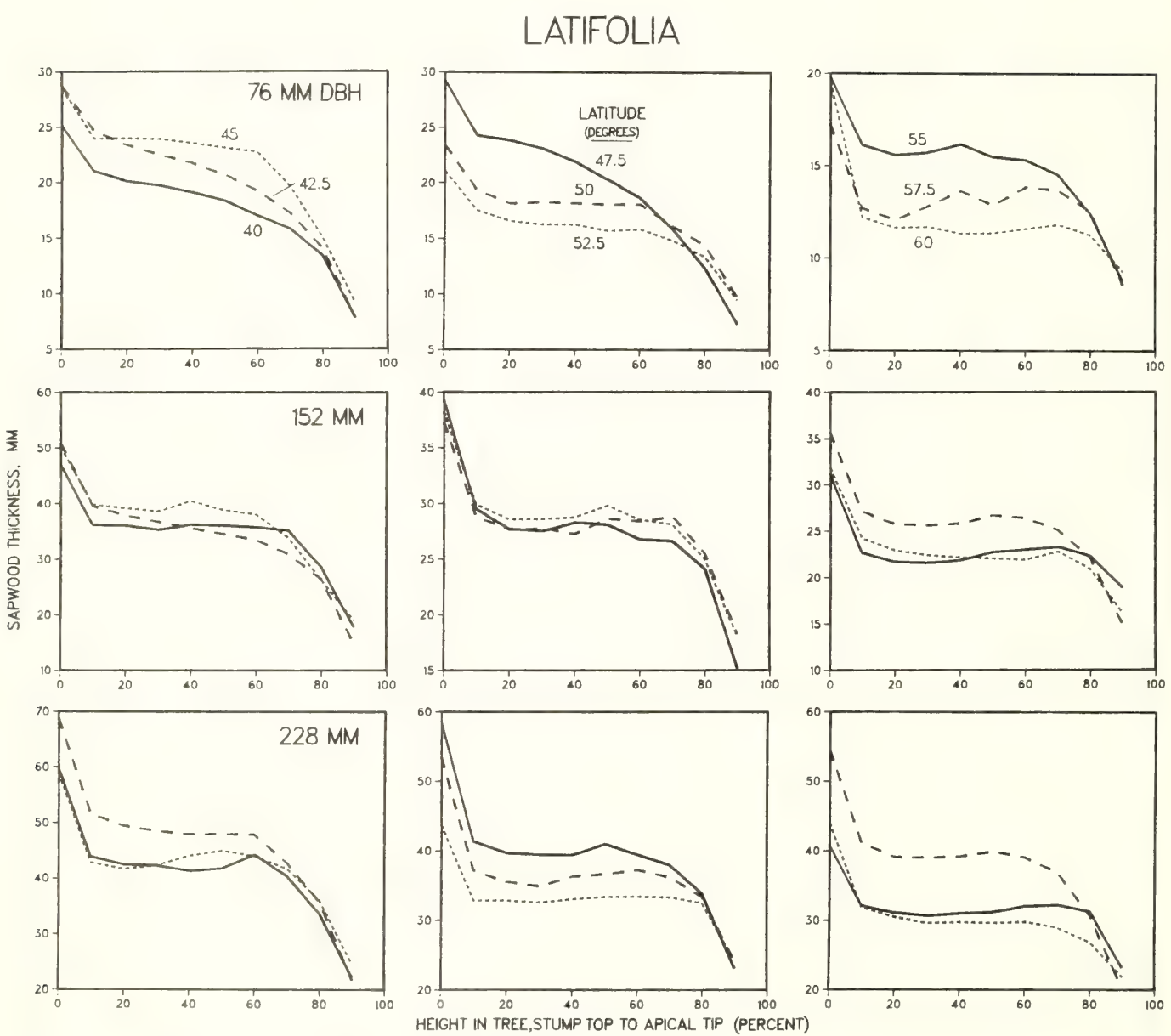


Figure 5-14—Sapwood thickness in *latifolia* trees of three diameters, related to height in tree and latitude.

Heartwood Volume as Percentage of Entire Stemwood Volume

Heartwood volume as a percentage of stemwood volume was unrelated to elevational zone, but was positively correlated with d.b.h., averaging 21.96 (16.22), 28.27 (15.28), and 34.20 (13.36) percent for trees of the three diameter classes (fig. 5-15).

Percentage of heartwood volume was also positively correlated with latitude, averaging least (17.4 percent) at 45 degrees and most (41.6 percent) at 60 degrees—with diameter data pooled; see figure 5-15.

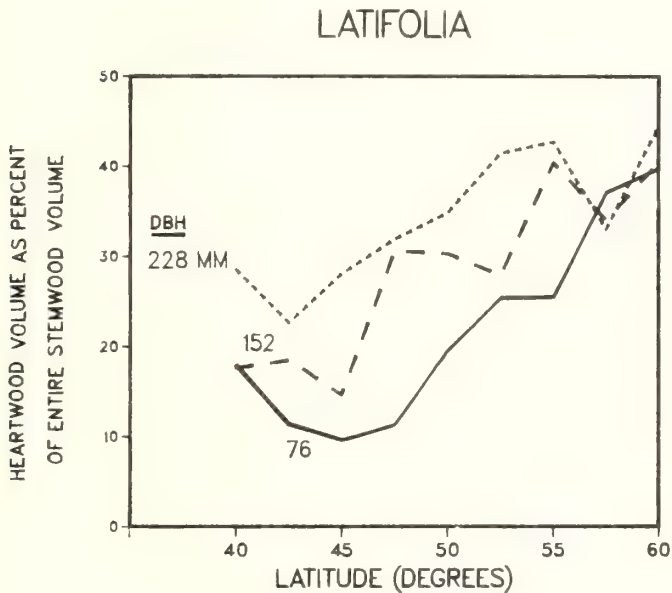


Figure 5-15—Heartwood as percentage of entire stemwood volume in latifolia trees of three diameters, related to latitude.

The following significant correlations (arbitrarily truncated at $r = 0.300$ to show the numerous factors involved) of heartwood volume as percentage of stemwood volume with other tree statistics are of interest:

Statistic	r
Heartwood as percentage of weight of bark-free stem, ovendry	0.997
Heartwood as percentage of weight of bark-free stem, green	.987
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	.941
Percentage moisture content of complete tree with foliage and cones	-.759
Percentage moisture content of complete tree without foliage or cones	-.745
Percentage moisture content of complete tree, wood only	-.737
Height (percent) of lowest tree disk in which heartwood does not occur	.735
Percentage moisture content of stem, wood plus bark	-.733

Statistic	r
Percentage moisture content of stemwood, tree average	-.722
Heartwood maximum diameter	.681
Percentage moisture content of wood of stump-root system	-.680
Percentage moisture content of stump-root system, wood plus bark	-.668
Green weight of heartwood	.635
Ovendry weight of heartwood	.630
Foliage as percentage of complete-tree weight, ovendry	-.626
Percentage moisture content of complete tree, bark only	-.564
Percentage moisture content of stembark, tree average	-.562
Stembark specific gravity	.554
Tree age at 152-mm stump height	.544
Percentage moisture content of foliage-free live branches	-.542
Height (m) of lowest tree disk in which heartwood does not occur	.541
Within-crown stemwood as percentage of entire stemwood volume	-.536
Crown ratio	-.510
Minimum sapwood thickness	-.479
Stem (wood plus bark) as percentage of complete-tree weight, ovendry	.477
Percentage moisture content of bark of stump-root system	-.436
Percentage moisture content of sapwood	-.428
Within-crown average stemwood taper, mm/m	.427
Percentage moisture content of live branchwood	-.416
Percentage moisture content of live branchbark	-.401
Tree height	.380
Ovendry weight of stem, wood plus bark	.373
Age of the lowest tree disk in which heartwood does not occur	-.370
Elevation, m	-.366
Height (percent) where maximum heartwood diameter occurs	-.358
Ovendry weight of stump-root system, wood plus bark	.341
Average branch diameter	.341
Height (m) where maximum heartwood diameter occurs	-.323
D.b.h.	.320
Percentage moisture content of heartwood	-.311

The foregoing tabulation suggests that percentage of heartwood volume tends to be largest in large-diameter, tall, heavy, old trees growing at low elevation (in meters as opposed to elevational zone within a latitudinal zone) with low crown ratios, large branches, and large within-crown stemwood taper.

Also, heartwood volume percentage tends to be greatest in trees of low moisture content having stembark of high specific gravity, a small percentage of complete-tree weight in foliage, but a large percentage in stemwood.

Heartwood as Percentage of Stemwood Volume by Level

Heartwood as percentage of stemwood volume varied with height in tree; from 22 to 37 percent at 152-mm stump height it increased to a maximum (28 to 42 percent) at about 10 percent of tree height, and then diminished more or less linearly toward the apical tip (fig. 5-16). At all levels in the tree, heartwood as percentage of stemwood volume was positively correlated with d.b.h. (fig. 5-16).

In low-elevation zones within latitudinal zones heartwood as percentage of stemwood volume was less—at all levels in the trees—than that found in medium- and high-elevation zones of that latitude (fig. 5-17).

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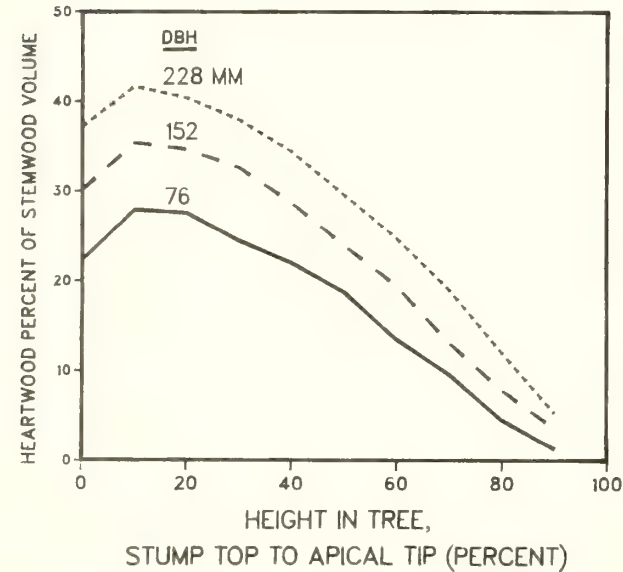


Figure 5-16—Heartwood as percentage of stemwood volume in *latifolia* trees of three diameters, related to height in tree.

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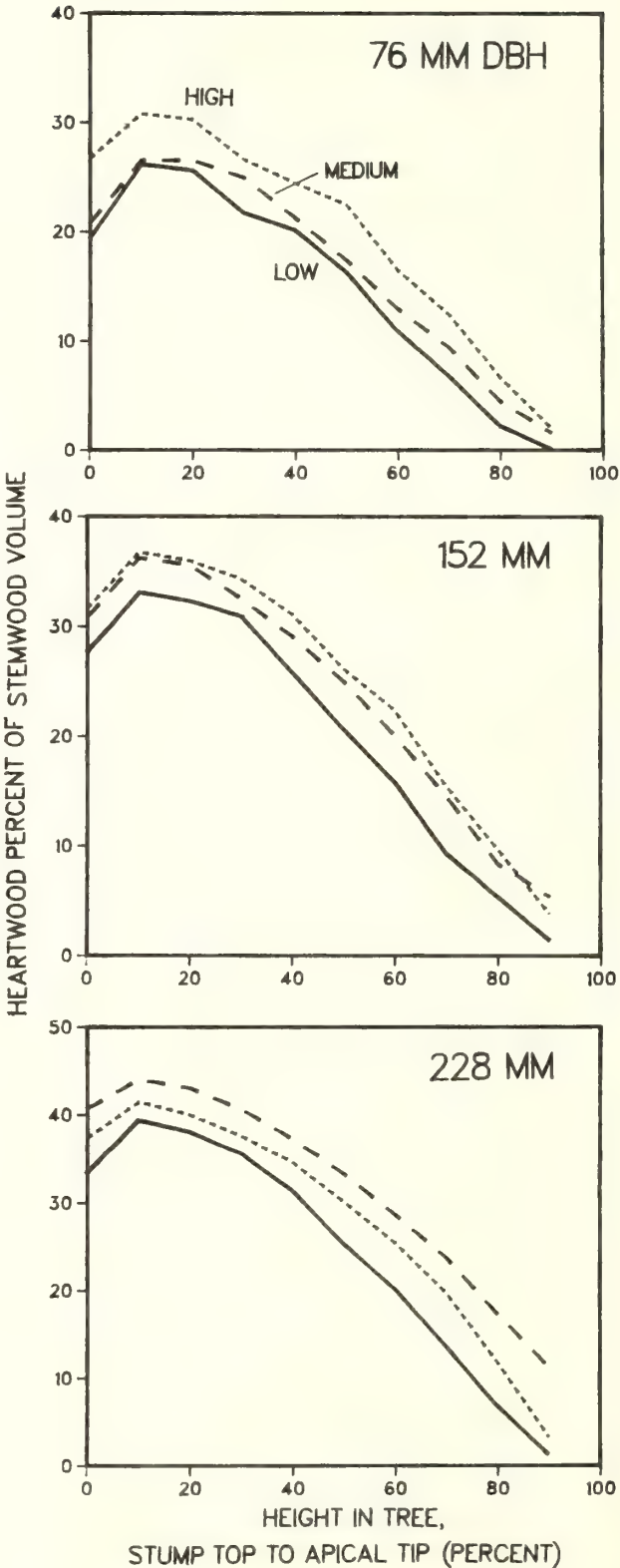


Figure 5-17—Heartwood as percentage of stemwood volume in *latifolia* trees of three diameters, related to height in tree and elevational zone.

Heartwood as percentage of stemwood volume was positively correlated with latitude; for example, at 10 percent of tree height—with diameter data pooled—the percentage averaged minimum (22.6 percent) at 42.5 degrees and maximum (48.3 percent) at 60 degrees (fig. 5-18).

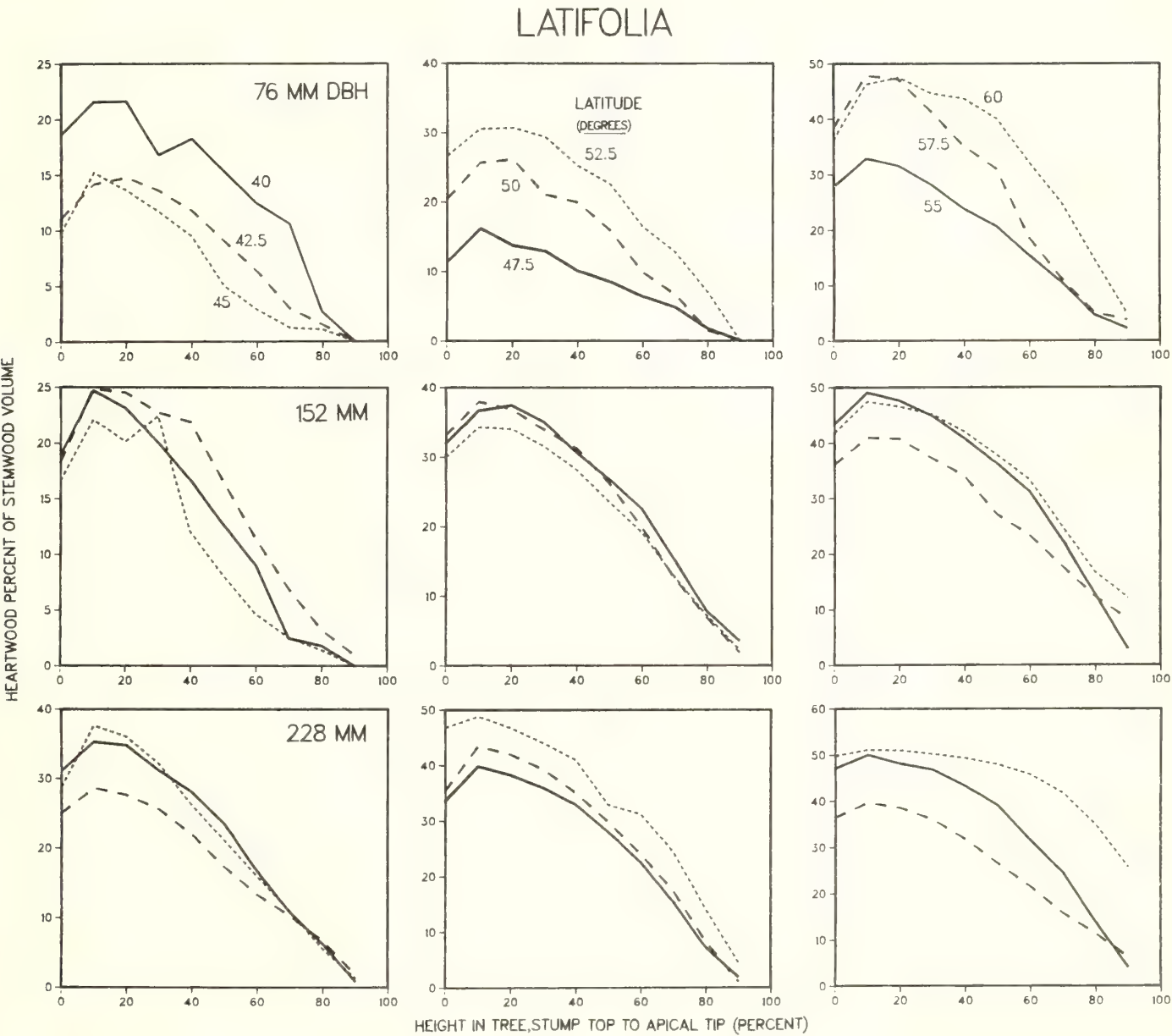


Figure 5-18—Heartwood as percentage of stemwood volume in *latifolia* trees of three diameters, related to height in tree and latitude.

Moisture Content of Entire Stemwood Component

Sapwood—Sapwood moisture content was not strongly related to elevational zone within a latitudinal zone. As noted in chapter 2, it averaged 119.3 percent, with standard deviation of 23.1 percent. The smallest trees had lowest sapwood moisture content, as follows:

D.b.h.	Moisture content and standard deviation	
mm	Percent	
76	110.1	(28.5)
152	121.7	(18.6)
228	126.1	(17.7)

This relationship changed at 45 degrees latitude, where trees of all three diameters had sapwood with the same moisture content, and at 47.5 degrees where sapwood moisture content was higher in 76-mm trees than in 228-mm trees (fig. 2-21). Sapwood moisture content averaged highest at latitude 42.5 degrees (139 percent), and lowest at 55 degrees (108 percent).

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the moisture content of entire sapwood with other tree statistics are of interest:

Statistic	<i>r</i>
Percentage moisture content of stemwood, tree average	0.886
Percentage moisture content of complete tree, wood only	.872
Percentage moisture content of stem, wood plus bark	.866
Percentage moisture content of complete tree without foliage or cones	.845
Percentage moisture content of complete tree with foliage and cones	.827
Stemwood specific gravity	-.689
Specific gravity of entire sapwood	-.678
Percentage moisture content of foliage-free live branches	.643
Percentage moisture content of wood of stump-root system	.620
Percentage moisture content of stump-root system, wood plus bark	.601
Percentage moisture content of live branchwood	.583
Minimum sapwood thickness	.533
Heartwood as percentage of weight of bark-free stem, green	-.480
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	-.474
Foliage as percentage of complete-tree weight, ovendry	.447
Percentage moisture content of live branchbark	.430

Statistic	<i>r</i>
Heartwood as percentage of stemwood volume	-.428
Live branch (wood plus bark) as percentage of complete-tree weight, ovendry	.416
Heartwood as percentage of weight of bark-free stem, ovendry	-.408
Stem (wood plus bark) as percentage of complete-tree weight, ovendry	-.403
Percentage moisture content of complete tree, bark only	.400
Stemwood d.i.b. at base of live crown	.391
Elevation, m	.371
Crown ratio	.367
Within-crown stemwood as percentage of entire stemwood volume	.365
Stembark specific gravity	-.362
Percentage moisture content of bark of stump-root system	.350
Ovendry foliage weight	.345
Percentage moisture content of stembark, tree average	.335
Height (percent) of lowest disk in which heartwood does not occur	-.313
Green weight of sapwood	.305

These data suggest that sapwood moisture content tends to be greatest in trees growing at high elevation (meters) with large crown ratios, heavy foliage, and a high percentage of complete-tree weight in foliage and branches, but a low percentage in stem (wood plus bark).

Also, sapwood moisture content is maximum in trees with wide sapwood, a low volume and weight percentage of heartwood, bark of high moisture content, and low specific gravity of stemwood, sapwood, and stembark.

The moisture content of sapwood has significant positive correlation with the moisture content of the complete tree without foliage and cones ($r = 0.845$), branches including bark (0.430), and stump-root system (0.601).

Moisture content of sapwood, while significantly correlated with that of heartwood, is not closely correlated ($r = 0.287$); it is not significantly correlated with foliage moisture content.

Heartwood—Moisture content of heartwood was not significantly related to elevational zone within a latitudinal zone. As noted in chapter 2, heartwood moisture content was much less than that of sapwood; it averaged 43.4 percent, with standard deviation of 5.7 percent. Heartwood moisture content was inversely correlated with d.b.h., averaging 47.2 (6.9), 41.9 (3.8), and 40.9 (3.8) percent in trees 76, 152, and 228 mm in d.b.h.

In contrast with sapwood, the smallest trees had highest heartwood moisture content at all latitudes; variation with latitude was less pronounced in heartwood than in sapwood—especially in larger trees (fig. 2-22).

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the moisture content of entire heartwood with other tree statistics are of interest:

Statistic	<i>r</i>
Percentage moisture content of stembark, tree average	0.560
Percentage moisture content of complete tree (bark only)	.546
Height (m) of lowest disk in which heartwood does not occur	-.544
Tree height	-.537
Height (percent) of lowest disk in which heartwood does not occur	-.485
Percentage moisture content of complete tree with foliage and cones	.469
Percentage moisture content of complete tree without foliage or cones	.468
Ovendry weight of sapwood	-.468
Percentage moisture content of stem, wood plus bark	.459
D.b.h.	-.449
Stembark specific gravity	-.448
Ovendry weight of stem, wood plus bark	-.446
Foliage as percentage of complete-tree weight, ovendry	.445
Ovendry weight of stump-root system, wood plus bark	-.441
Green weight of sapwood	-.440
Heartwood maximum diameter	-.435
Percentage moisture content of complete tree, wood only	.421
Percentage moisture content of stemwood, tree average	.418
Percentage moisture content of bark of stump-root system	.414
Percentage moisture content of stump-root system, wood plus bark	.404
Height in tree (m) where minimum sapwood thickness occurs	-.392
Percentage moisture content of wood of stump-root system	.383
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	-.373
Stem (wood plus bark) as percentage of complete-tree weight, ovendry	-.372
Stump-root system (wood plus bark) as percentage of complete-tree weight, ovendry	.370
Stemwood d.i.b. at base of live crown	-.345
Specific gravity of entire sapwood	-.340
Bark thickness at 152-mm stump height	-.333
Within-crown stemwood as percentage of entire stemwood volume	.333
Ovendry foliage weight	-.328
Ovendry weight of heartwood	-.324
Number of live branches	-.323
Stemwood specific gravity	-.322
Ovendry weight of live branches, wood plus bark	-.316

Statistic	<i>r</i>
Heartwood as percentage of stemwood volume	-.311
Green weight of heartwood	-.304
Taproot length	-.304

The foregoing data suggest that heartwood moisture content tends to be greatest in short, small-diameter trees with few branches of light weight, and stump-root systems (with short taproots) and foliage that comprise a large percentage of complete-tree weight.

As noted previously, heartwood moisture content is not significantly correlated with sapwood moisture content. It is, however, significantly and positively correlated with the moisture content of stembark ($r = 0.560$), complete tree (0.469), and wood of the stump-root system (0.383).

It is negatively correlated with sapwood ovendry weight ($r = -0.468$), stembark specific gravity (-0.448), heartwood maximum diameter (-0.435), ovendry weight of heartwood (-0.324), stemwood specific gravity (-0.322), and both ovendry weight of heartwood and heartwood as percentage of stemwood volume (-0.323 and -0.311 , respectively).

Surprisingly, heartwood moisture content is not significantly correlated with heartwood specific gravity.

Moisture Content of Sapwood by Level

Sapwood moisture content was least (averaging 110 percent) in the lowest 10 percent of the tree stems, increased more or less linearly to a maximum (averaging 136 percent) at about 80 percent of tree height, and then diminished slightly toward the apical tip (fig. 5-19).

Sapwood moisture content was positively correlated with d.b.h. at all heights in the trees (fig. 5-19).

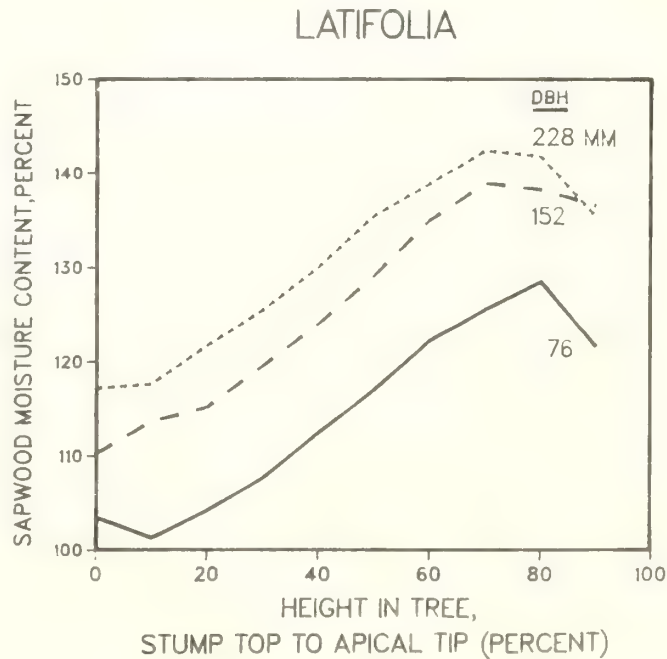


Figure 5-19—Sapwood moisture content in *latifolia* trees of three diameters, related to height in tree.

Sapwood moisture content at most levels was negatively correlated with latitude. For example, at 40 percent of tree height sapwood moisture content averaged 146 percent at 42.5 degrees latitude (diameter data pooled), but averaged only 115 percent at 60 degrees (fig. 5-20).

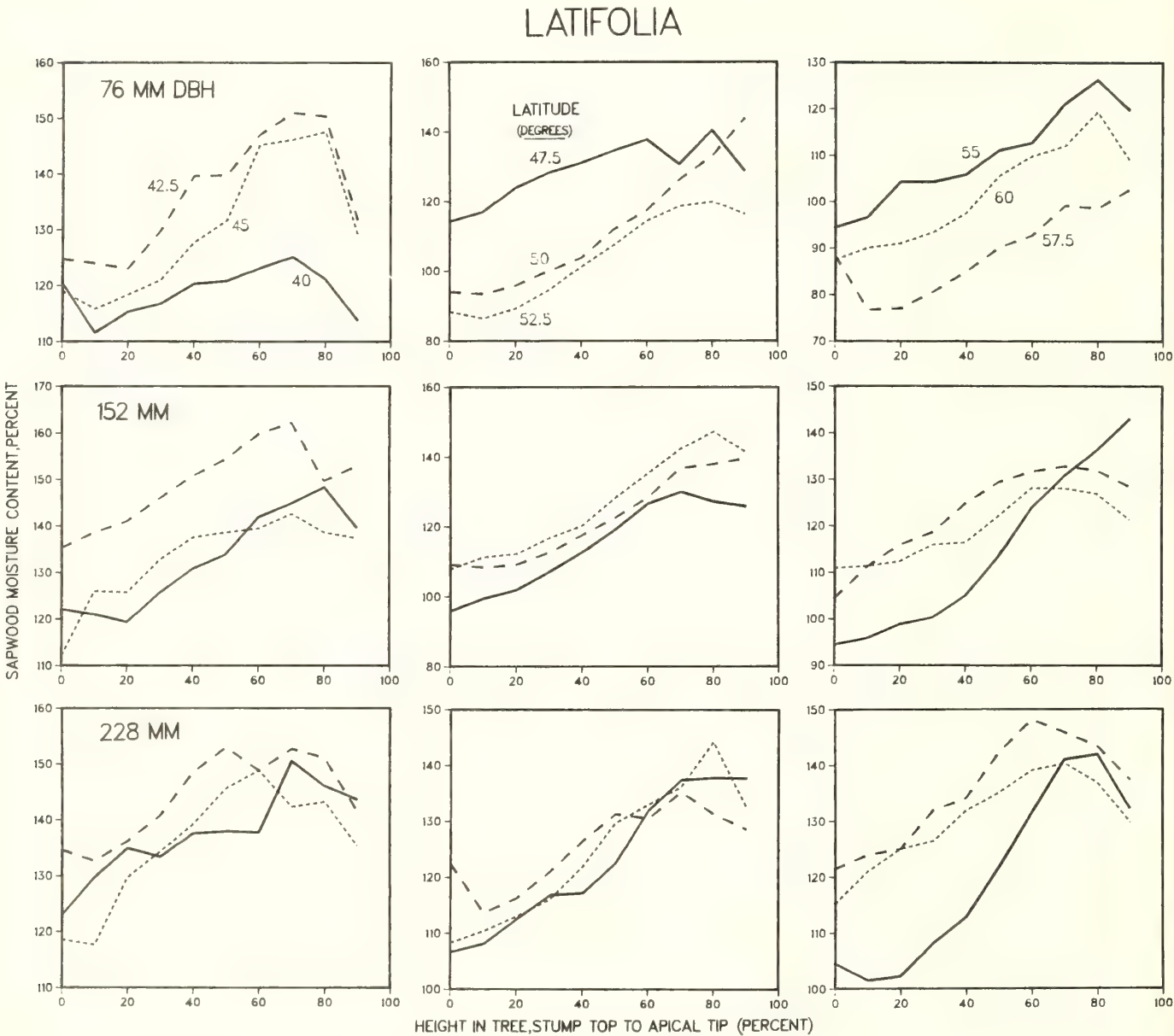


Figure 5-20—Sapwood moisture content in *latifolia* trees of three diameters, related to height in tree and latitude.

Moisture Content of Heartwood by Level

Heartwood moisture content was minimum (averaging 42 percent with diameter data pooled) at 152-mm stump height, and increased curvilinearly to a maximum (averaging 52 percent) at 90 percent of tree height (fig. 5-21).

Below about 70 percent of tree height, heartwood in 152- and 228-mm trees had moisture content positively correlated with elevational zone (fig. 5-22).

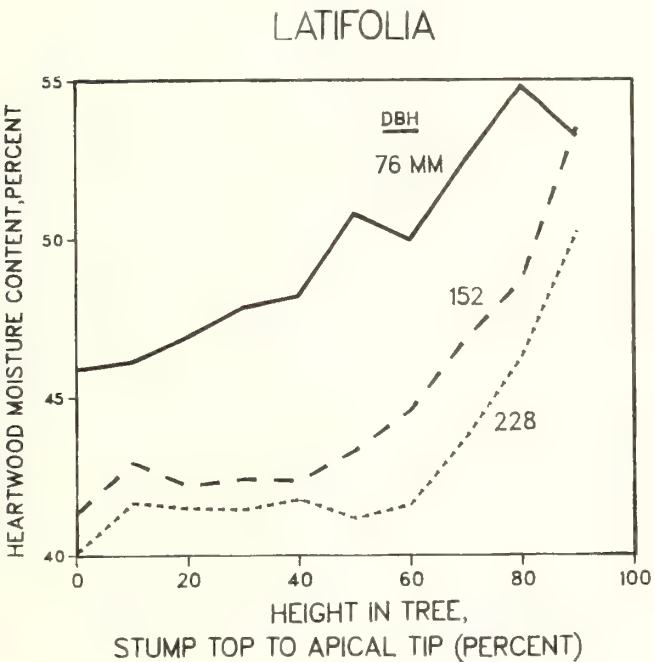


Figure 5-21—Heartwood moisture content in *latifolia* trees of three diameters, related to height in tree.

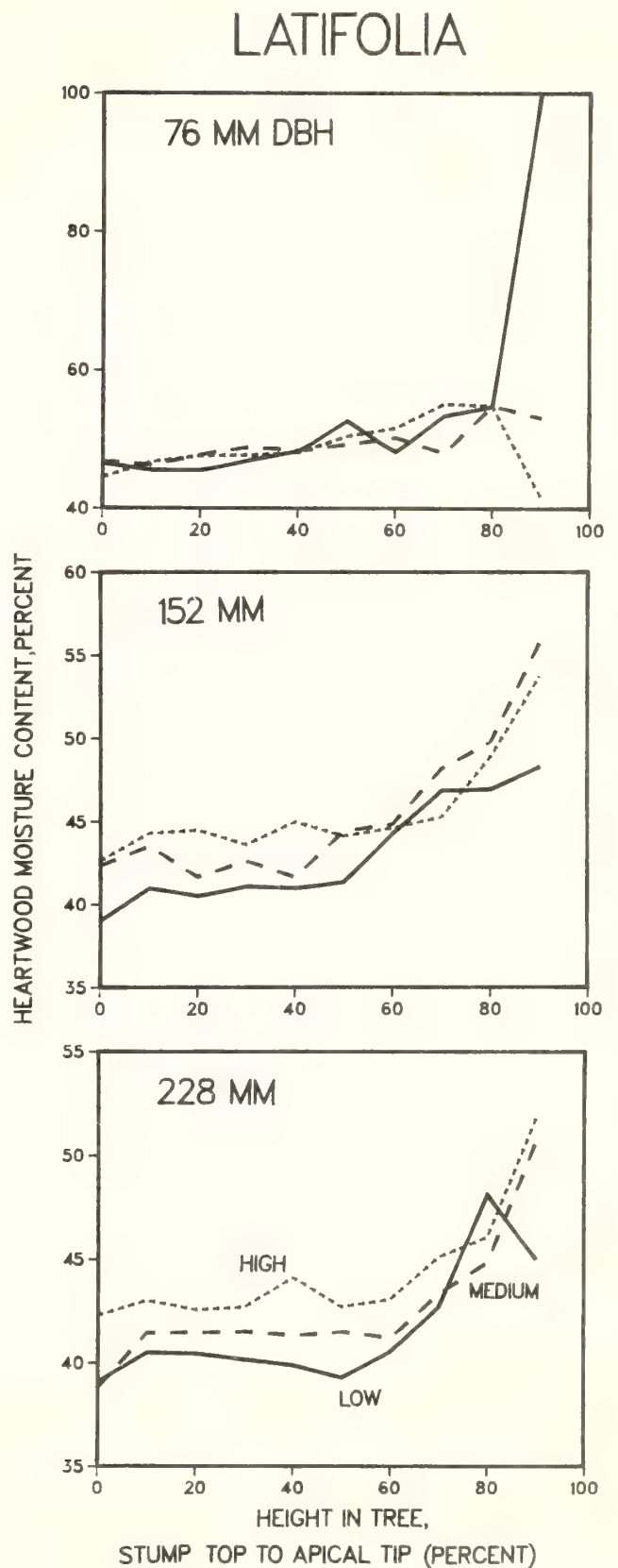


Figure 5-22—Heartwood moisture content in *latifolia* trees of three diameters, related to height in tree and elevational zone.

The relationships between latitude and heartwood moisture content at various heights in the trees were complex, and differed with d.b.h. (fig. 5-23).

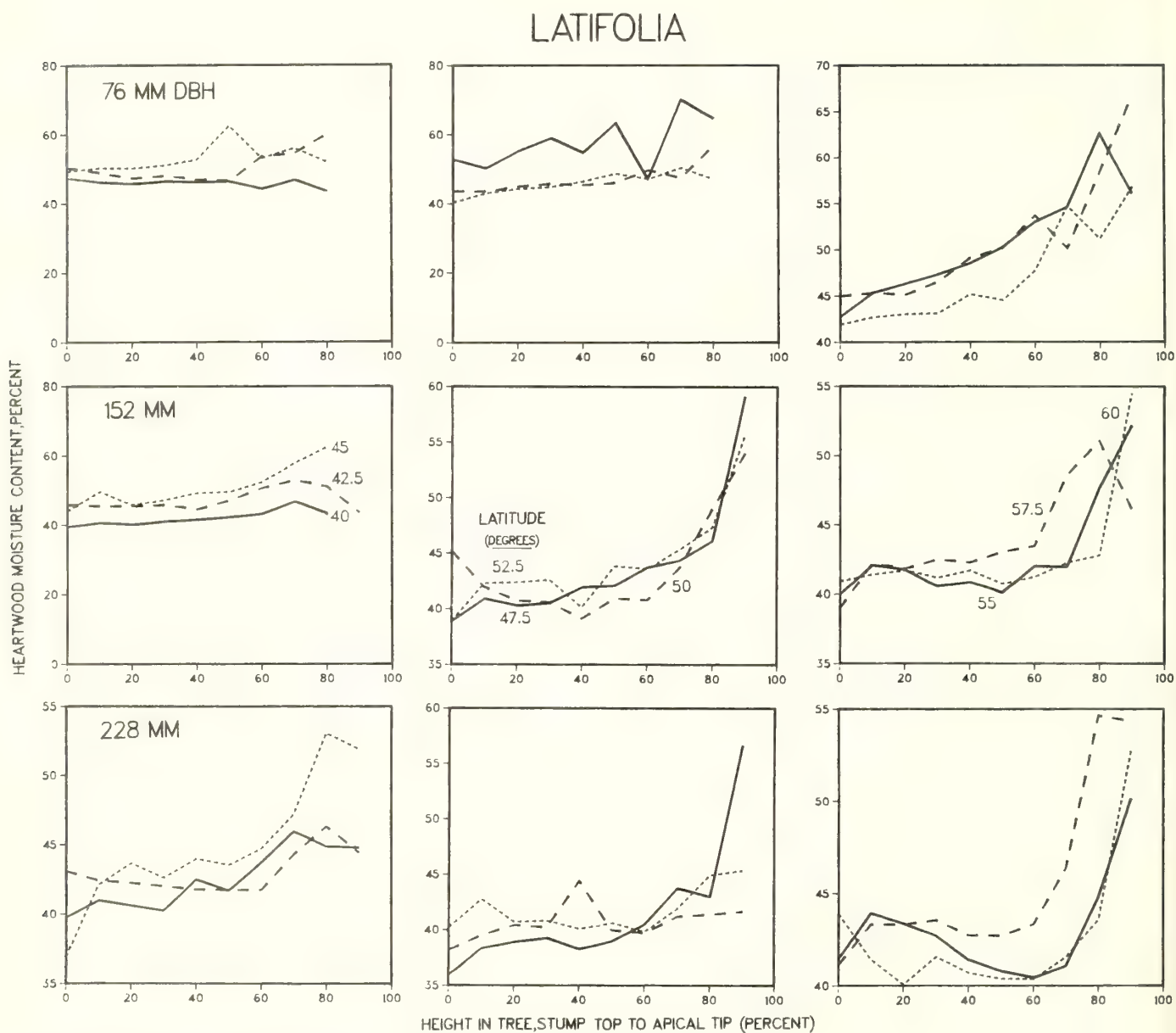


Figure 5-23—Heartwood moisture content in *latifolia* trees of three diameters, related to height in tree and latitude.

Weight of Sapwood in Entire Stem

Green—As noted in chapter 4, sapwood green weight was positively correlated with d.b.h. (fig. 4-59), averaging 14.37 (4.27), 91.34 (23.70), and 226.16 (60.87) kg for trees of the three diameter classes. It was negatively correlated with elevational zone, particularly in 228-mm trees, as follows:

Elevational zone	76 mm d.b.h.	152 mm d.b.h.	228 mm d.b.h.
----- Kilograms -----			
Low	15.19	94.82	248.38
Medium	14.39	94.61	221.86
High	13.53	84.60	208.23

Sapwood green weight was also negatively correlated with latitude, diminishing slightly in northern latitudes (fig. 4-59).

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the green weight of sapwood with other tree statistics are of interest:

Statistic	r
Ovendry weight of sapwood	0.992
Ovendry weight of stem, wood plus bark	.926
D.b.h.	.907
Ovendry weight of stump-root system, wood plus bark	.899
Stemwood d.i.b. at base of live crown	.843
Tree height	.835
Ovendry foliage weight	.823
Ovendry weight of live branches, wood plus bark	.776
Height (m) of lowest tree disk in which heartwood does not occur	.770
Number of live branches	.694
Heartwood maximum diameter	.690
Average branch diameter	.685
Taproot length	.652
Minimum sapwood thickness	.652
Ovendry weight of heartwood	.648
Green weight of heartwood	.637
Average growth-ring width at 152-mm stump height	.618
Height in tree (m) where minimum sapwood thickness occurs	.613

Statistic	r
Stump-root system (wood plus bark) as percentage of complete-tree weight, ovendry	-.588
Bark thickness at 152-mm stump height	.539
Number of cones on tip 305 mm of top 25 branches	.534
Ovendry weight of dead branches	.526
Specific gravity of entire heartwood	-.522
Percentage moisture content of heartwood	-.440
Within-crown average stemwood taper, mm/m	.367
Percentage moisture content of stembark, tree average	-.366
Height (percent) of lowest tree disk in which heartwood does not occur	.351
Below-crown average stemwood taper, mm/m	.339
Percentage moisture content of sapwood	.305

Sapwood green weights are obviously positively correlated with d.b.h. ($r = 0.907$), with tree height (0.835), and with sapwood moisture content (0.305).

Also, sapwood green weights are maximum in fast-growing trees with heavy foliage and numerous large, heavy live branches bearing numerous cones, heavy dead branches, and thick bark at stump height—all of which are attributes of many large, tall trees. Additionally, sapwood green weights tend to be greatest in trees with long taproots, large stemwood diameter at the base of the live crown, and large stemwood taper—both within and below crown.

Sapwood green weights are negatively correlated with stump-root as percentage of complete-tree weight ($r = -0.588$), heartwood specific gravity (-0.522), heartwood moisture content (-0.440), and stembark moisture content (-0.366).

Ovendry—As noted in chapter 4, ovendry sapwood weight was positively correlated with d.b.h., averaging 6.89 (2.00), 41.45 (10.78), and 99.81 (24.88) kg for trees of the three diameter classes. In 228-mm trees, ovendry sapwood weight was negatively correlated with elevational zone, averaging 109.91, 98.13, and 91.40 kg in low, medium, and high zones, respectively.

As with green sapwood weight, ovendry weight had a slight negative correlation with latitude (fig. 4-60).

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the ovendry weight of sapwood with other tree statistics are of interest:

Statistic	r
Green weight of sapwood	0.992
Ovendry weight of stem, wood plus bark	.952
D.b.h.	.916
Ovendry weight of stump-root system, wood plus bark	.916
Tree height	.867
Stemwood d.i.b. at base of live crown	.833
Height (m) of lowest tree disk in which heartwood does not occur	.808
Ovendry foliage weight	.806
Ovendry weight of live branches, wood plus bark	.762
Heartwood maximum diameter	.730
Ovendry weight of heartwood	.697
Number of live branches	.695
Average branch diameter	.692
Green weight of heartwood	.686
Taproot length	.656
Height in tree (m) where minimum sapwood thickness occurs	.622
Minimum sapwood thickness	.618
Average growth-ring width at 152-mm stump height	.611
Stump-root system (wood plus bark) as percentage of complete-tree weight, ovendry	-.602
Bark thickness at 152-mm stump height	.557
Number of cones on tip 305 mm of top 25 branches	.545
Ovendry weight of dead branches	.513
Specific gravity of entire heartwood	-.502
Percentage moisture content of heartwood	-.468
Percentage moisture content of stembark, tree average	-.402
Height (percent) of lowest tree disk in which heartwood does not occur	.382
Within-crown average stemwood taper, mm/m	.376
Below-crown average stemwood taper, mm/m	.327
Percentage moisture content of complete tree, bark only	-.320

Sapwood ovendry weights, like sapwood green weights, are positively correlated with d.b.h. ($r = 0.916$), and with tree height (0.867). Also, sapwood ovendry weights are maximum in fast-growing trees with heavy foliage and numerous large, heavy live branches bearing numerous cones, heavy dead branches, and thick bark at stump height—all of which are frequently attributes of large, tall trees.

As with green weights, sapwood ovendry weights are also greatest in trees with long taproots, large stemwood diameter at the base of the live crown, and large stemwood taper—both within and below crown.

Sapwood ovendry weights are negatively correlated with stump-root system percentage of complete-tree weight ($r = -0.602$), specific gravity of entire heartwood (-0.502), percentage moisture content of heartwood (-0.468), and percentage moisture content of bark of complete tree (-0.320).

Weight of Heartwood in Entire Stem

Green—As noted in chapter 4, weight of green heartwood was positively correlated with d.b.h. (fig. 4-61), averaging 3.26 (2.51), 25.28 (16.15), and 76.85 (37.92) kg for trees 76, 152, and 228 mm in d.b.h. Generally it was also positively correlated with elevational zone, averaging as follows for trees of the three diameters:

Elevational zone	76 mm	152 mm	228 mm
	- - - - - Kilograms - - - - -		
Low	2.94	22.02	73.74
Medium	3.28	26.34	81.32
High	3.56	27.46	75.50

Green heartwood weight was also positively correlated with latitude; the relationship was most pronounced in large trees (fig. 4-61).

The following significant relationships (arbitrarily truncated at $r = 0.400$) of the green weight of heartwood with other tree statistics are of interest:

Statistic	r
Ovendry weight of heartwood	0.999
Heartwood maximum diameter	.911
Ovendry weight of stem, wood plus bark	.874
Height (m) of lowest tree disk in which heartwood does not occur	.809
Ovendry weight of stump-root system, wood plus bark	.804
D.b.h.	.773
Tree height	.767
Average branch diameter	.708
Ovendry weight of sapwood	.686
Green weight of sapwood	.637
Heartwood as percentage of stemwood volume	.635
Heartwood as percentage of stemwood weight, ovendry	.624
Ovendry weight of live branches, wood plus bark	.590
Stemwood d.i.b. at base of live crown	.582
Heartwood as percentage of bark-free stem, green	.569
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	.561
Ovendry foliage weight	.523
Percentage moisture content of stembark, tree average	-.520
Height (percent) of lowest tree disk in which heartwood does not occur	.518
Tree age at 152-mm stump height	.512
Number of cones on tip 305 mm of top 25 branches	.505

Statistic	<i>r</i>
Stump-root system (wood plus bark) as percentage of complete-tree weight, ovendry	-.504
Within-crown average stem taper, mm/m	.490
Percentage moisture content of complete tree, bark only	-.477
Height in tree (m) where minimum sapwood thickness occurs	.468
Ovendry weight of dead branches	.443
Taproot length	.427
Age of the lowest tree disk in which heartwood does not occur	-.423
Foliage as percentage of complete-tree weight, ovendry	-.418
Stembark specific gravity	.405
Number of live branches	.402

Heartwood green weights, in addition to being positively correlated with d.b.h. ($r = 0.773$), tree height (0.767), heartwood maximum diameter (0.911), and heartwood height in tree (0.809), are also positively correlated with the ovendry weight of the stump-root system (0.804), live branch weight (0.590), stemwood diameter at the base of the live crown (0.582), and foliage weight (0.523).

Heartwood green weight is negatively correlated with foliage percent of complete-tree ovendry weight, however.

Additionally, heartwood green weight tends to be greatest in trees with numerous cones, large within-crown taper, heavy dead branches, long taproots, dense stem-bark, and numerous large live branches.

Heartwood green weight is negatively correlated with stembark percentage moisture content ($r = -0.520$), stump-root system percent of complete-tree weight (-0.504), and age of lowest tree disk in which heartwood does not occur (-0.423).

Ovendry—As noted in chapter 4, ovendry heartwood weight was also positively correlated with d.b.h. (fig. 4-62), averaging 2.25 (1.78), 17.86 (11.34), and 54.27 (26.23) kg for trees of the three diameter classes. It was also generally positively correlated with elevational zone, averaging as follows for trees of the three diameters:

Elevational zone	76 mm	152 mm	228 mm
- - - - - Kilograms - - - - -			
Low	2.02	15.83	52.61
Medium	2.29	18.65	57.59
High	2.46	19.09	52.61

As with green heartwood, weight of ovendry heartwood was positively correlated with latitude; the relationship was most pronounced in trees of large diameter (fig. 4-62).

The following significant correlations (arbitrarily truncated at $r = 0.400$) of the ovendry weight of entire heartwood with other tree characteristics are of interest:

Statistic	<i>r</i>
Green weight of heartwood	0.999
Heartwood maximum diameter	.913
Ovendry weight of stem, wood plus bark	.883
Height (m) of lowest tree disk in which heartwood does not occur	.815
Ovendry weight of stump-root system, wood plus bark	.812
D.b.h.	.778
Tree height	.775
Average branch diameter	.706
Ovendry weight of sapwood	.697
Green weight of sapwood	.648
Heartwood as percentage of stemwood volume	.630
Heartwood as percentage of stemwood weight, ovendry	.619
Ovendry weight of live branches, wood plus bark	.596
Stemwood d.i.b. at base of live crown	.588
Heartwood as percentage of stemwood weight, green	.562
Heartwood as percentage of stem diameter at point of maximum heartwood diameter	.558
Ovendry foliage weight	.529
Percentage moisture content of stembark, tree average	-.523
Height (percent) of lowest tree disk in which heartwood does not occur	.518
Number of cones on tip 305 mm of top 25 branches	.509
Stump-root system as percentage of complete-tree weight, ovendry	-.508
Tree age at 152-mm stump height	.503
Within-crown average stemwood taper, mm/m	.486
Percentage moisture content of complete tree, bark only	-.481
Height in tree (m) where minimum sapwood thickness occurs	.476
Ovendry weight of dead branches	.450
Taproot length	.434
Foliage as percentage of complete-tree weight, ovendry	-.420
Age of the lowest tree disk in which heartwood does not occur	-.418
Number of live branches	.410
Stembark specific gravity	.407

These correlations vary only slightly from the tabulation for green heartwood weights, so the comments made about green heartwood weight relationships apply equally to ovendry weight of heartwood.

Heartwood as Percentage of Weight of Entire Stemwood

Green—Heartwood as percentage of green stemwood was positively correlated with d.b.h., averaging 18.4 (14.6), 21.6 (13.4), and 25.7 (11.9) percent for trees 76, 152, and 228 mm in diameter (fig. 5-24). Generally it was also positively correlated with elevational zone within a latitudinal zone, averaging as follows for trees of the three diameters (see also fig. 5-26):

Elevational zone	76 mm	152 mm	228 mm
----- Percent -----			
Low	16.5	18.9	23.2
Medium	17.7	22.2	27.6
High	21.0	23.8	26.4

In all three diameter classes heartwood as percentage of green stemwood weight was positively correlated with latitude (fig. 5-24). With diameter data pooled, heartwood content was minimum at 42.5 degrees (13.0 percent) and maximum at 60 degrees (33.9 percent).

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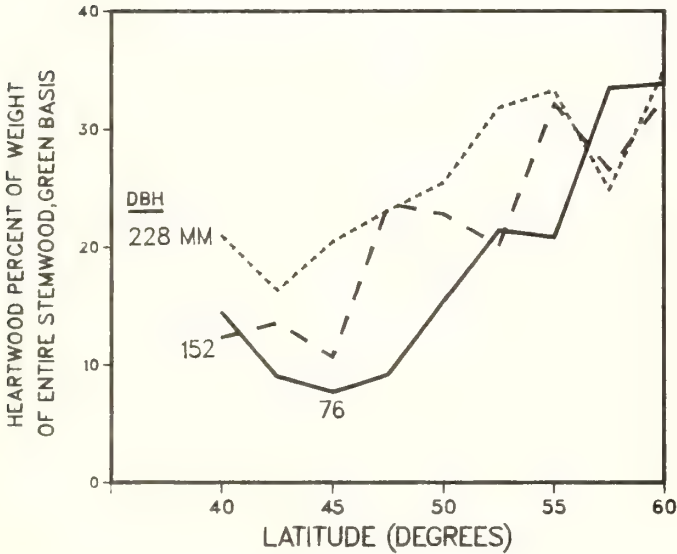


Figure 5-24—Green heartwood as percentage of entire green stemwood weight in *latifolia* trees of three diameters, related to latitude.

The following significant correlations (arbitrarily truncated at $r = 0.300$) of the heartwood percent of the green and ovendry weights of entire stemwood with other tree characteristics are of interest:

Statistic	<i>r</i>	
	Ovendry	Green
Heartwood as percentage of stemwood volume	0.997	0.987
Heartwood as percentage of weight of stemwood, green	.988	1.000
Heartwood as percentage of weight of stemwood, ovendry	1.000	.988
Heartwood as percentage of stem diameter at height of maximum heartwood diameter	.937	.917
Percentage moisture content of complete tree with foliage and cones	-.747	-.761
Percentage moisture content of complete tree without foliage or cones	-.733	-.749
Height (percent) of lowest tree disk in which heartwood does not occur	.730	.681
Percentage moisture content of complete tree, wood only	-.727	-.748
Percentage moisture content of stem, wood plus bark	-.720	-.738
Percentage moisture content of stemwood, tree average	-.711	-.733
Percentage moisture content of stump-root system, wood only	-.675	-.675
Heartwood maximum diameter	.673	-.600
Percentage moisture content of stump-root system, wood plus bark	-.663	-.657
Green weight of heartwood	.624	.569
Ovendry weight of heartwood	.619	.562
Foliage as percentage of complete-tree weight, ovendry	-.604	-.590
Tree age at 152-mm stump height	.560	.516
Percentage moisture content of complete tree, bark only	-.546	-.519
Percentage moisture content of stembark, tree average	-.545	-.509
Stembark specific gravity	.537	.525
Percentage moisture content of foliage-free live branches, wood plus bark	-.531	-.569
Within-crown stemwood as percentage of entire stemwood volume	-.526	-.508

Statistic	<i>r</i>	
	Ovendry	Green
Height (m) of lowest tree disk in which heartwood does not occur	.517	.443
Crown ratio	-.496	-.486
Minimum sapwood thickness	-.488	-.541
Stem (wood plus bark) as percentage of dry complete-tree weight	.444	.449
Within-crown average stemwood taper, mm/m	.441	.387
Percentage moisture content of bark of stump-root system	-.423	-.401
Percentage moisture content of live branchwood	-.408	-.460
Percentage moisture content of sapwood	-.408	-.480
Percentage moisture content of live branchbark	-.390	-.405
Age of lowest tree disk in which heartwood does not occur	-.364	-.344
Elevation, m	-.363	-.361
Ovendry weight of stem, wood plus bark	.357	
Height (percent) where maximum heartwood diameter occurs	-.352	-.327
Tree height	.352	
Average branch diameter	.345	
Ovendry weight of stump-root system, wood plus bark	.330	
Height (m) where maximum heartwood diameter occurs	-.325	-.317
D.b.h.	.312	

Heartwood as a percentage of green weight of entire stemwood, in addition to the obvious positive correlation with heartwood as a percentage of stem volume and heartwood as a percentage of stem diameter at height of maximum heartwood diameter, is also positively correlated with stembark specific gravity ($r = 0.525$), tree age at stump height (0.516), stem (wood plus bark) as a percentage of complete-tree ovendry weight (0.449), and within-crown stem taper (0.387).

The negative correlations in the foregoing tabulation suggest that heartwood as a percentage of green weight of entire stemwood is maximum at low elevation (elevation in meters, as opposed to elevational zone within a latitudinal zone) in trees with low moisture content, foliage comprising a small percentage of complete-tree weight, thin sapwood, and low crown ratio. Heartwood as a percentage of green weight of entire stemwood is also negatively correlated with the age of the lowest tree disk in which heartwood does not occur ($r = -0.344$).

Ovendry—As noted in chapter 4, heartwood ovendry weight as a percentage of stemwood was positively correlated with d.b.h. (fig. 4-63), averaging 22.6 (16.3), 28.8 (15.3), and 34.6 (13.4) percent for trees 76, 152, and 228 mm in diameter. It was also positively correlated with latitude, averaging—with diameter data pooled—minimum (18.0 percent) at 42.5 degrees and maximum (43.0 percent) at 60 degrees (fig. 4-63).

Within latitudinal zones there was a tendency for trees in low-elevation zones to have a smaller percentage of

heartwood by ovendry weight than those in medium or high zones, as follows:

Elevational zone	<i>r</i>		
	76 mm	152 mm	228 mm
Low	20.7	26.0	31.5
Medium	21.4	29.4	36.9
High	25.8	30.9	35.5

Significant correlations (arbitrarily truncated at $r = 0.300$) of heartwood as a percentage of ovendry weight of entire stemwood with other tree characteristics are shown in the tabulation of similar data on a green basis. These correlations vary only slightly from those applicable to green weight percentages; the comments made about green heartwood weight percentages therefore apply equally to ovendry weight percentages.

Additionally, heartwood as percentage of ovendry weight of entire stemwood is positively correlated with ovendry weight of stem, including both wood and bark ($r = 0.357$); ovendry weight of stump-root system, including wood and bark (0.330); tree height (0.352); average branch diameter (0.355); and d.b.h. (0.312).

Heartwood as Percentage of Stemwood Weight by Level

Green—With diameter data pooled, heartwood as percentage of green stemwood weight averaged about 24 percent at stump height of 152 mm, increased to about 28 percent at 10 percent of tree height, and then decreased curvilinearly toward the apical tip (fig. 5-25). At all levels in the tree, heartwood green weight proportion of stemwood was positively correlated with d.b.h.

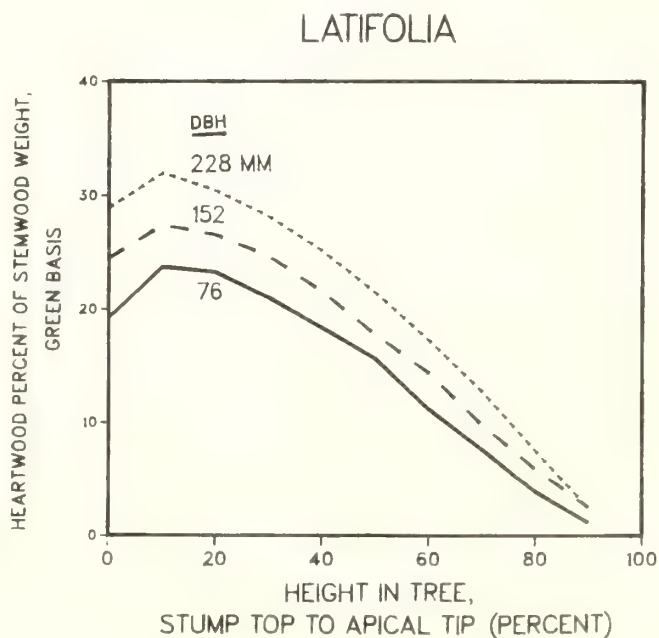


Figure 5-25—Green heartwood as percentage of green stemwood weight in *latifolia* trees of three diameters, related to height in tree.

Within latitudinal zones, trees from low-elevation zones had less heartwood as a percentage of green stemwood weight at all stem levels than those from medium and high zones (fig. 5-26).

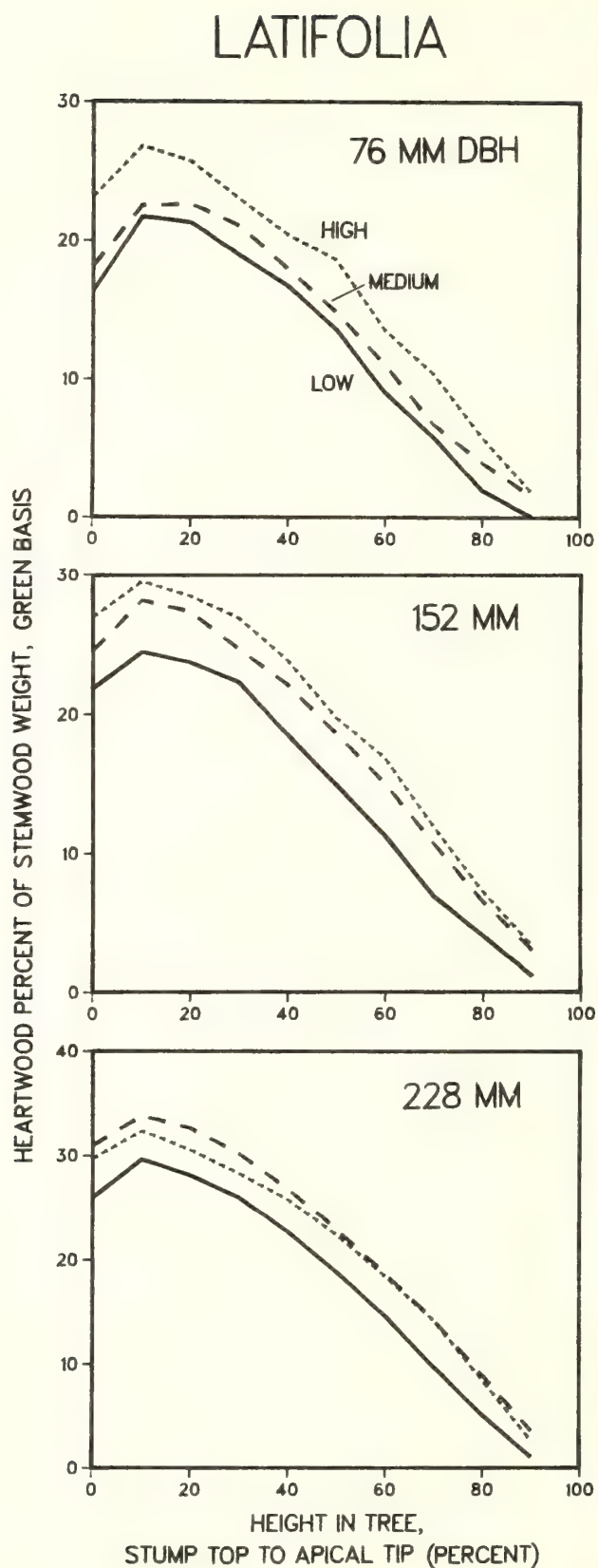


Figure 5-26—Green heartwood as percentage of green stemwood weight in *latifolia* trees of three diameters, related to height in tree and elevational zone.

In general, heartwood as a percentage of green stemwood weight was greatest in northern latitudes and least in southern, but relationships varied with d.b.h. and height in tree (fig. 5-27).

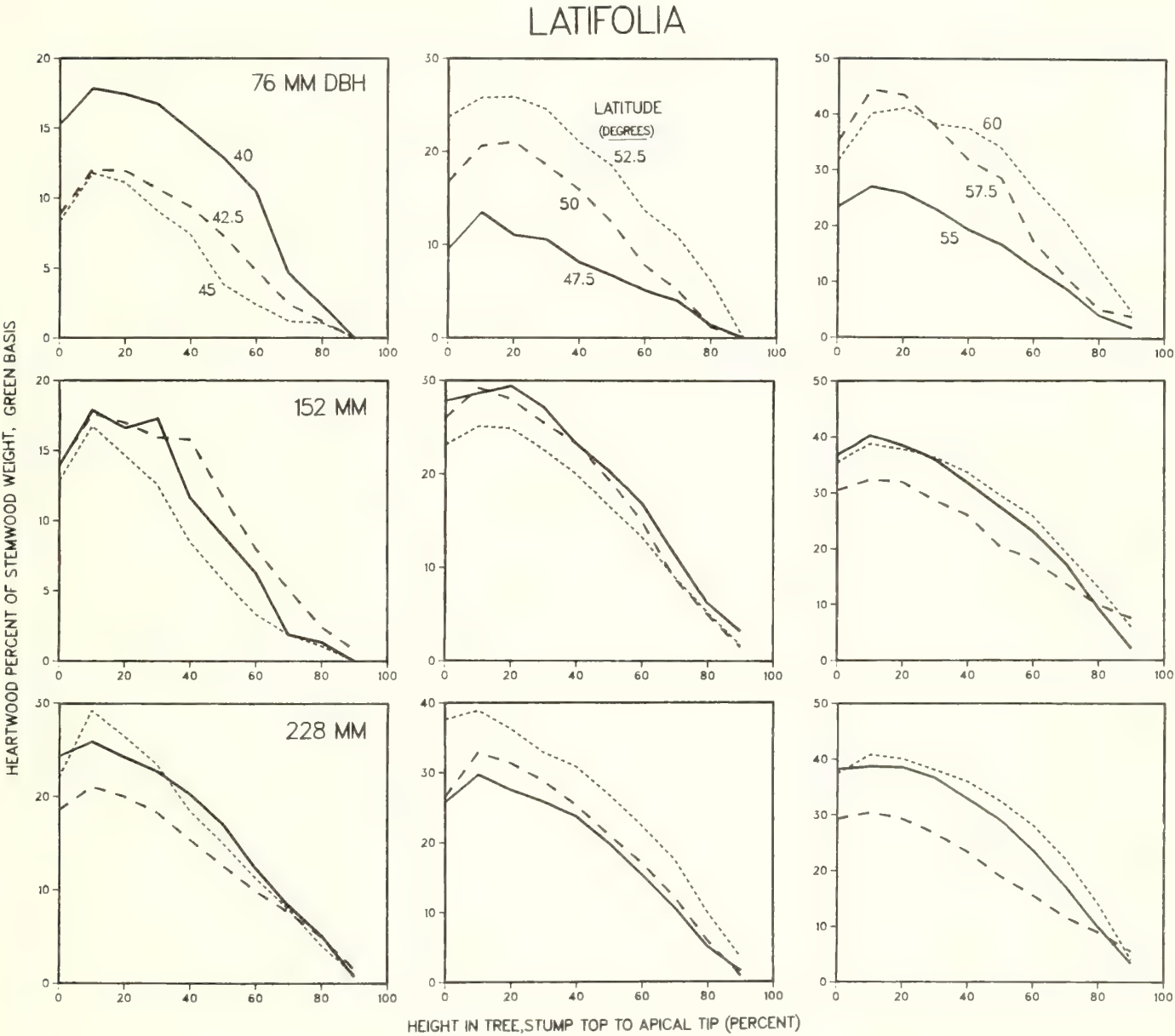


Figure 5-27—Green heartwood as percentage of green stemwood weight in *latifolia* trees of three diameters, related to height in tree and latitude.

Ovendry—With diameter data pooled, heartwood as a percentage of ovendry stemwood weight averaged about 30 percent at stump height of 152 mm, increased to about 34 percent at 10 percent of tree height, and then decreased curvilinearly toward the apical tip (fig. 5-28). As with green weight proportion, at all levels in the tree heartwood ovendry weight proportion of stemwood weight was positively correlated with d.b.h. (fig. 5-28).

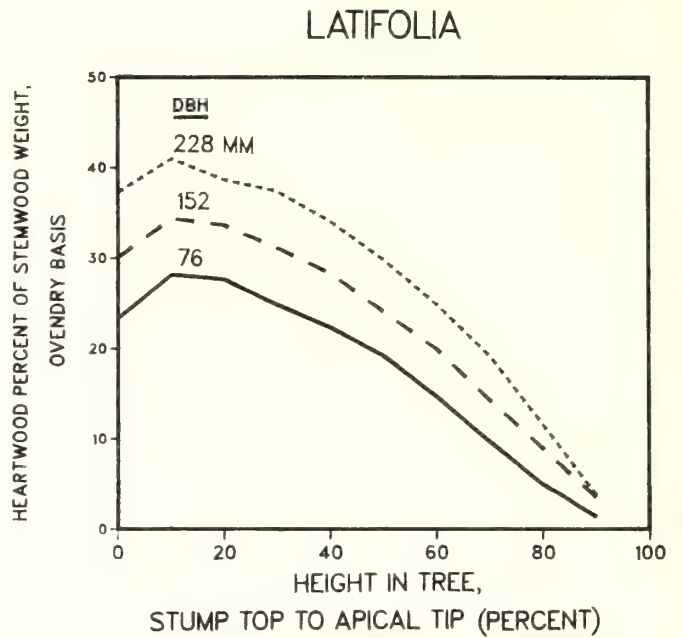


Figure 5-28—Ovendry heartwood as percentage of ovendry stemwood weight in *latifolia* trees of three diameters, related to height in tree.

As with green weight proportion, heartwood as a percentage of ovendry stemwood weight tended to be greatest in northern latitudes and least in southern, but relationships varied with d.b.h. and height in tree (fig. 5-29).

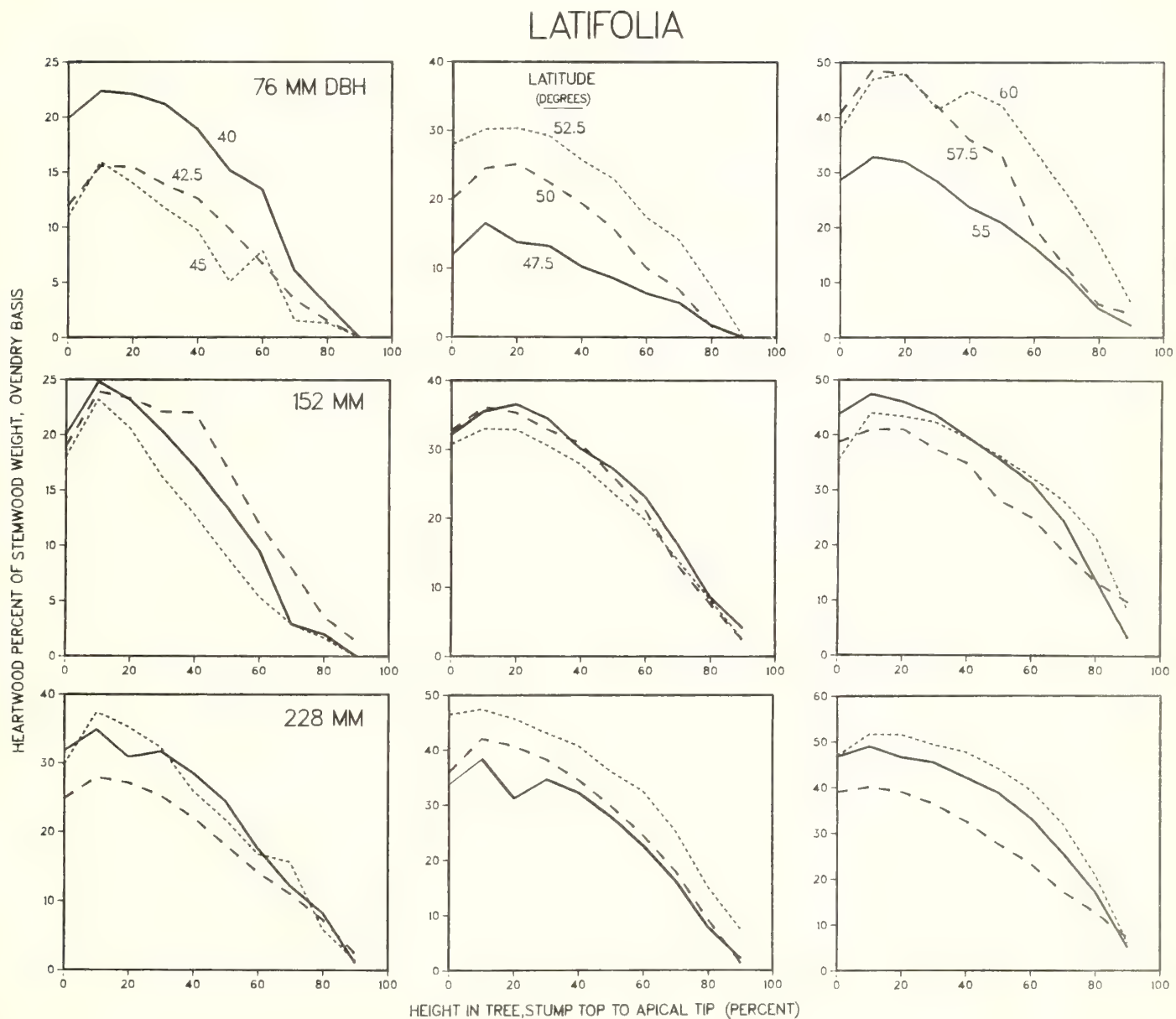


Figure 5-29—Ovendry heartwood as percentage of ovendry stemwood weight in *latifolia* trees of three diameters, related to height in tree and latitude.

Specific Gravity of Sapwood in Entire Stem

As noted in chapter 4, sapwood specific gravity in the entire stem (ovendry weight and green volume basis) was less than that of heartwood, averaging 0.414, with standard deviation of 0.034. Like whole-stemwood specific gravity it was negatively correlated with d.b.h., averaging 0.423 (0.039), 0.415 (0.032), and 0.405 (0.030) for trees 76, 152, and 228 mm in d.b.h.; diameter-related differences were more pronounced in northern than in southern latitudes (fig. 4-58).

Sapwood specific gravity averaged maximum (0.425 to 0.435) at middle latitudes of 47.5 through 55 degrees, and minimum (0.396) at 40 degrees (fig. 4-58).

The following significant correlations (arbitrarily truncated at $r = 0.200$ to show most relationships involved) of sapwood specific gravity with other tree statistics are of interest:

Statistic	<i>r</i>
Stemwood specific gravity	0.967
Percentage moisture content of sapwood	-.678
Percentage moisture content of complete tree (wood only)	-.566
Percentage moisture content of stemwood, tree average	-.566
Percentage moisture content of complete tree without foliage or cones	-.555
Percentage moisture content of stem (wood plus bark)	-.551
Percentage moisture content of complete tree with foliage and cones	-.537
Percentage moisture content of wood of stump-root system	-.481
Percentage moisture content of stump-root system (wood plus bark)	-.461
Stem (wood plus bark) as percentage of complete-tree weight, ovendry	.456
Specific gravity of entire heartwood	.449
Percentage moisture content of foliage-free live branches (wood plus bark)	-.447
Live branch (wood plus bark) as percentage of complete-tree weight, ovendry	-.432
Foliage as percentage of complete-tree weight, ovendry	-.400
Percentage moisture content of live branchwood	-.375
Crown ratio	-.359
Below-crown average stemwood taper, mm/m	-.358
Minimum sapwood thickness	-.350
Percentage moisture content of heartwood	-.340

Statistic	<i>r</i>
Stembark specific gravity	.333
Elevation, m	-.329
Percentage moisture content of live branchbark	-.326
Stemwood d.i.b. at base of live crown	-.324
Within-crown stemwood percentage of entire stemwood volume	-.316
Percentage moisture content of bark of stump-root system	-.287
Average branch diameter	-.287
Ovendry foliage weight	-.277
Percentage moisture content of complete tree (bark only)	-.276
Heartwood as percentage of stemwood diameter at height of maximum heartwood diameter	.273
Height (percent) of lowest tree disk in which heartwood does not occur	.261
Average branch angle	.252
Heartwood as percentage of weight of stemwood, green	.238
Heartwood as percentage of stemwood volume	.238
Ovendry weight of live branches (wood plus bark)	-.235
Average growth-ring width at 152-mm stump height	-.225
D.b.h.	-.213
Percentage moisture content of stembark, tree average	-.206
Heartwood as percentage of weight of stemwood, ovendry	.201

These data suggest that sapwood specific gravity tends to be highest at low elevation in small-diameter, slow-growing trees with a high percentage of complete-tree weight in the stem, low crown ratio, a small percentage of complete-tree weight in foliage, a low weight of foliage, little stemwood taper below crown, thin sapwood, small stemwood diameter at the base of the live crown, and small-diameter lightweight branches having high branch angles.

Sapwood specific gravity is positively correlated with heartwood specific gravity ($r = 0.449$), stembark specific gravity (0.333), heartwood as a percentage of stemwood diameter at height of maximum heartwood diameter (0.273), height of heartwood in tree (0.261), and heartwood as a percentage of stemwood weight and volume (0.238).

It is negatively correlated with sapwood moisture content (-0.678) and moisture content of most other tree components.

Specific Gravity of Sapwood by Level

With diameter data pooled, sapwood specific gravity based on ovendry weight and green volume averaged 0.449 at stump height of 152 mm, decreased to a minimum of 0.387 at 70 percent of tree height, and then increased to 0.399 at 90 percent of tree height. At all levels, it was negatively correlated with d.b.h. (fig. 5-30).

As noted previously, sapwood specific gravity averaged maximum at latitudes from 47.5 through 55 degrees, and minimum at 40 degrees; figure 5-31 relates latitude to sapwood specific gravity at various heights in trees of the three diameters.

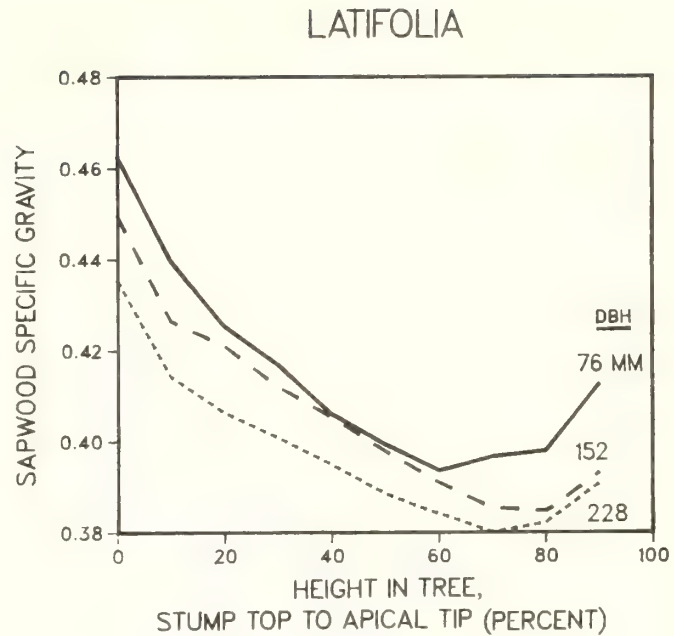


Figure 5-30—Sapwood specific gravity (based on green volume and unextracted ovendry weight) in *latifolia* trees of three diameters, related to height in tree.

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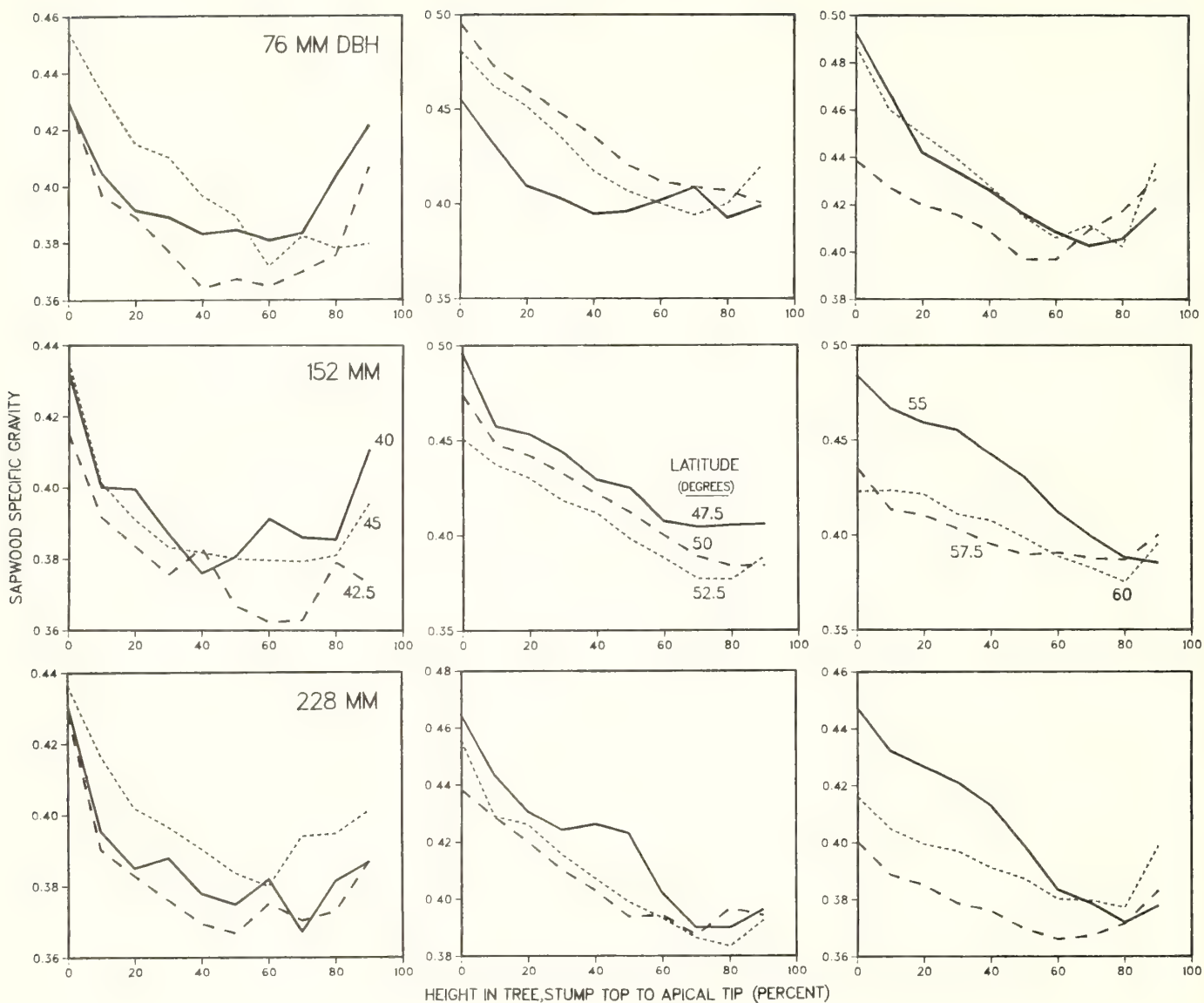


Figure 5-31—Sapwood specific gravity (based on green volume and unextracted oven-dry weight) in *latifolia* trees of three diameters, related to latitude.

Specific Gravity of Heartwood in Entire Stem

As noted in chapter 4, heartwood specific gravity in entire stems averaged 0.434, with standard deviation of 0.034, based on unextracted ovendry weight and green volume. It was unrelated to elevational zone and latitude, but was negatively correlated with d.b.h., as follows:

D.b.h.	Specific gravity and standard deviation	
<i>mm</i>		
76	0.459	(0.038)
152	.430	(.022)
228	.412	(.022)

The following significant correlations (arbitrarily truncated at $r = 0.200$ to show most relationships involved) of heartwood specific gravity with other tree statistics are of interest. In addition to the tree statistics listed, content of extractives likely has a significant effect on heartwood specific gravity, but such determinations—although scheduled—had not been made at the time this paper was written.

Statistic	<i>r</i>
D.b.h.	-0.560
Stemwood specific gravity	.548
Green weight of sapwood	-.522
Stemwood d.i.b. at base of live crown	-.514
Tree height	-.502
Ovendry weight of sapwood	-.502
Height (m) of lowest tree disk in which heartwood does not occur	-.495
Ovendry weight of stump-root system (wood plus bark)	-.489
Heartwood maximum diameter	-.480
Ovendry weight of stem (wood plus bark)	-.478
Ovendry foliage weight	-.454
Specific gravity of entire sapwood	.449
Average branch diameter	-.446
Ovendry weight of live branches (wood plus bark)	-.432
Average growth-ring width at 152-mm stump height	-.432
Stump-root system (wood plus bark) as percentage of complete-tree weight, ovendry	.394
Height in tree (m) where minimum sapwood thickness occurs	-.367
Number of live branches	-.359
Green weight of heartwood	-.349
Taproot length	-.348
Height (percent) of lowest tree disk in which heartwood does not occur	-.348
Ovendry weight of heartwood	-.347

Statistic	<i>r</i>
Ovendry weight of dead branches	-.331
Number of cones on tip 305 mm of top 25 branches	-.331
Minimum sapwood thickness	-.313
Average branch angle	.311
Bark thickness at 152-mm stump height	-.295
Percentage moisture content of stembark, tree average	.289
Within-crown average stemwood taper, mm/m	-.282
Age of the lowest tree disk in which heartwood does not occur	.279
Percentage moisture content of sapwood	-.271
Foliage as percentage of complete-tree weight, ovendry	.261
Below-crown average stemwood taper, mm/m	-.257
Heartwood as percentage of stemwood diameter at height of maximum heartwood diameter	-.248
Percentage moisture content of complete tree (bark only)	.218
Heartwood as percentage of stemwood volume	-.203

The foregoing tabulation suggests that heartwood has highest specific gravity in small-diameter, short, slow-growing trees with thin sapwood and with thinnest sapwood occurring close to ground level, thin bark at stump height, small-diameter branches with large branch angles in lightweight crowns having few branches and few cones, few dead branches, short taproots, little stemwood taper within or below crown, and with foliage comprising a large percentage of complete-tree weight. Unlike sapwood, the specific gravity of heartwood is not significantly correlated with its moisture content, as follows:

Statistic	Moisture content of	
	Sapwood	Heartwood
	<i>r</i>	<i>r</i>
Specific gravity of sapwood	-0.678	-0.340
Specific gravity of heartwood	-.271	N.S.

Heartwood specific gravity is, however, positively correlated with stump-root system (wood plus bark) as percentage of complete-tree ovendry weight ($r = 0.394$), percentage moisture content of stembark (0.289), and age of lowest tree disk in which heartwood does not occur (0.279). Also, heartwood has highest specific gravity in trees with small heartwood maximum diameter in which heartwood does not extend far up the stem; that is, heartwood specific gravity is negatively correlated with both weight and volume of heartwood in a tree.

Specific Gravity of Heartwood by Level

The pattern of variation in heartwood specific gravity with height in tree is significantly different than that of sapwood (compare figs. 5-30 and 5-32). With diameter data pooled, heartwood had average specific gravity of 0.482 at a stump height of 152 mm, sharply decreased to a minimum of 0.412 at 30 percent of tree height, and then increased to a near maximum (0.478) at 90 percent of tree height.

The specific gravity of heartwood at all levels except 90 percent was lowest in trees of 228 mm d.b.h., and highest in 76-mm trees (fig. 5-32).

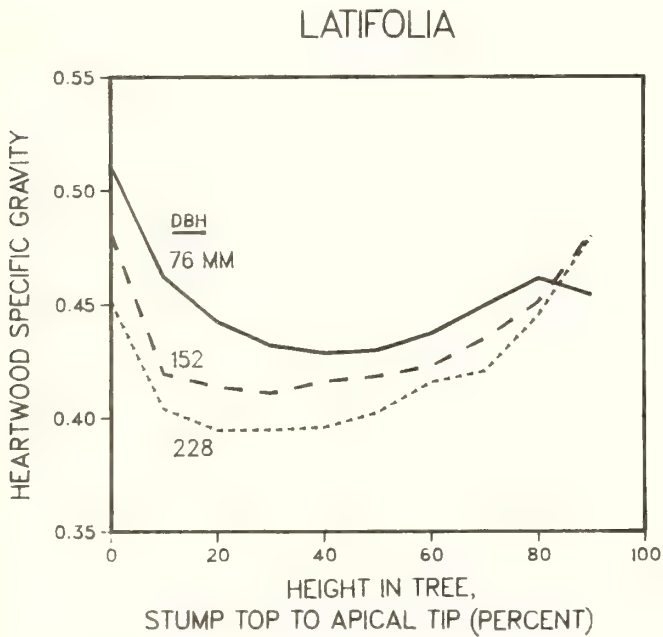


Figure 5-32—Heartwood specific gravity (based on green volume and unextracted oven-dry weight) in *latifolia* trees of three diameters, related to height in tree.

5-6 RESULTS—MURRAYANA

As noted in previous chapters, the three d.b.h. classes of *murrayana* trees averaged 76 mm with standard deviation of 1.8 mm, 151 mm with standard deviation of 2.9 mm, and 229 mm with standard deviation of 3.9 mm. All were selected at medium elevation, which for the four latitudes averaged as follows (fig. 1-1):

Latitude	Elevation	General location
Degrees	Meters	
37.5	2,402	Just east of Yosemite National Park
40	1,676	Vicinity of Quincy, CA
42.5	2,006	Southwest of Paisley, OR
45	1,148	North of Breitenbush, OR

Because the entire *murrayana* sample totaled but 36 trees, correlations between tree characteristics are not noted as they were for *latifolia* trees.

Heartwood Occurrence

Age of Lowest Tree Disk Where Heartwood Does Not Occur—With data on all trees pooled, the age of the lowest tree disk in which heartwood did not appear averaged 14.78 years, with standard deviation of 7.77 years. This age was unrelated to latitude but was inversely correlated with d.b.h., averaging 20.17 (7.99), 13.67 (5.26), and 10.5 (6.90) years for trees 76, 152, and 228 mm in diameter.

Height in the Tree at Which Heartwood No Longer Occurs, Percent—For all 36 *murrayana* trees, height in tree at which heartwood did not occur averaged 76.4 percent, with standard deviation of 17.8 percent. This percentage was unrelated to latitude, but was positively correlated with d.b.h., averaging 60.8 (16.2), 80.0 (15.4), and 88.3 (8.4) percent for trees of the three diameters.

Height in the Tree at Which Heartwood No Longer Occurs, Meters—The lowest height (meters) in trees at which heartwood did not occur was positively correlated with d.b.h., averaging 4.65 (2.08), 11.26 (4.38), and 16.60 (4.75) m for trees of the three diameter classes. This height was also positively correlated with latitude (fig. 5-33), averaging 3 to 6 m higher at 45 degrees than at 37.5 degrees.

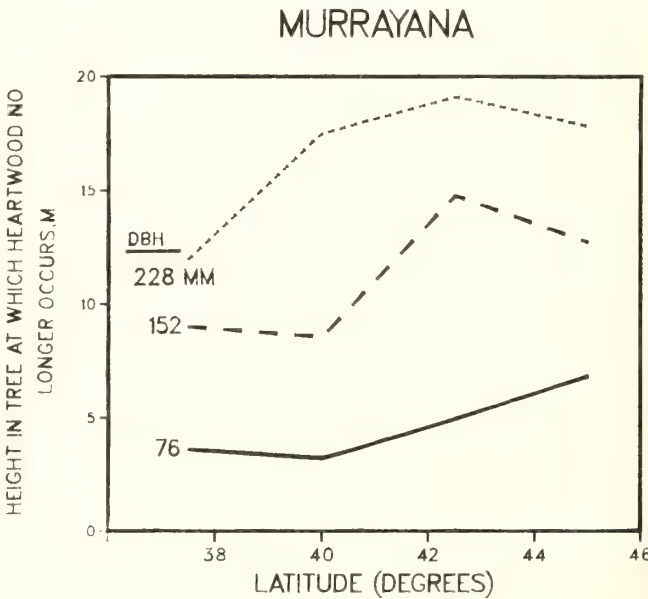


Figure 5-33—Height in tree at which heartwood does not occur in *murrayana* trees of three diameters, related to latitude.

Heartwood Maximum Diameter and Location

Heartwood Maximum Diameter—Heartwood maximum diameter was positively correlated with d.b.h., averaging 26.7 (11.1), 66.8 (22.6), and 108.3 (30.0) mm for trees of the three diameter classes. This maximum diameter was also positively correlated with latitude, particularly in 228-mm trees where the smallest was 64.3 mm at 37.5 degrees and the largest 134.7 at 42.5 degrees (fig. 5-34).

MURRAYANA

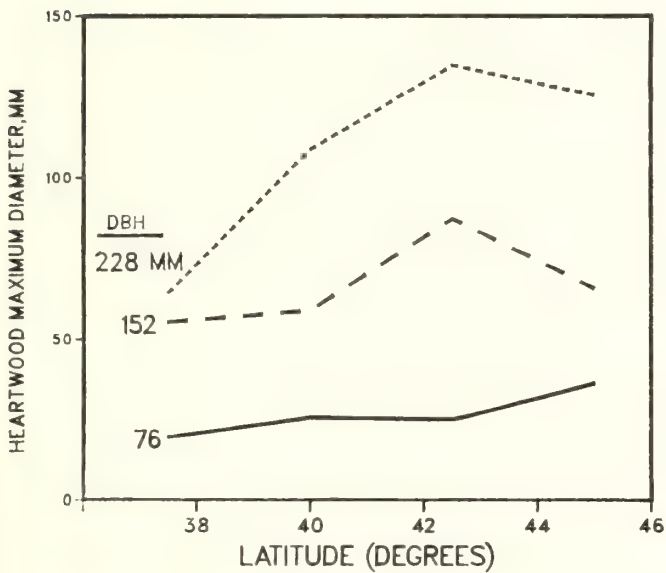


Figure 5-34—Heartwood maximum diameter in *murrayana* trees of three diameters, related to latitude.

Height at Which Maximum Heartwood Diameter Occurs, Percent—The proportion of tree height at which heartwood diameter was maximum was unrelated to d.b.h., averaging 7.5 percent, with standard deviation of 6.9 percent for all 36 trees. This height proportion did, however, vary significantly with latitude; it was greatest (11.1 percent) at 37.5 degrees and least (2.2 percent) at 40 degrees (fig. 5-35).

MURRAYANA

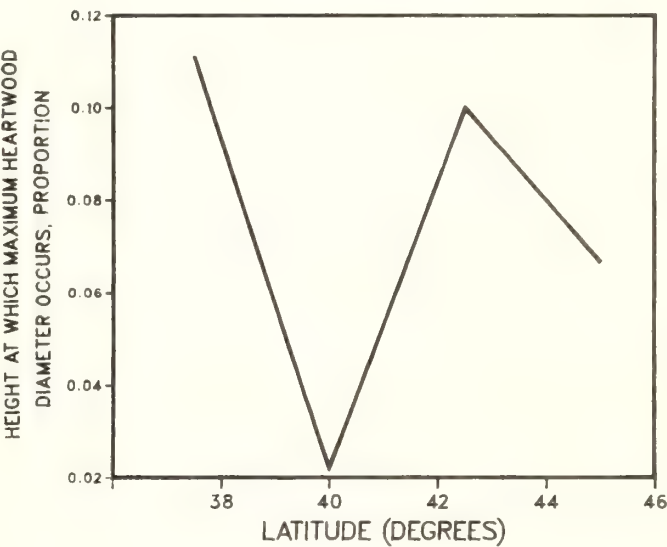


Figure 5-35—Proportion of tree height at which maximum heartwood diameter occurs in *murrayana* trees, related to latitude (diameter data pooled).

MURRAYANA

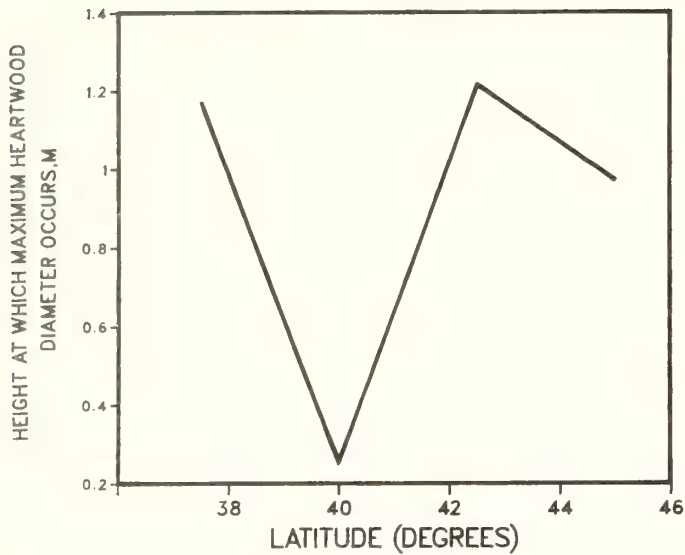


Figure 5-36—Height (meters) at which maximum heartwood diameter occurs in *murrayana* trees, related to latitude (diameter data pooled).

Height at Which Maximum Heartwood Diameter Occurs, Meters—Similarly, the height (meters) at which maximum heartwood diameter occurred did not vary significantly with d.b.h., averaging 0.90 m, with standard deviation of 0.83 m for all 36 trees. It was highest in trees sampled at 37.5 and 42.5 degrees (1.2 m) and lowest in those from 40 degrees (0.3 m); see figure 5-36.

Heartwood as Percentage of Stem Diameter, at Height of Maximum Heartwood Diameter—Heartwood as a percentage of stemwood diameter at height of maximum heartwood diameter averaged 42.8 percent, with standard deviation of 15.1 percent. Differences related to diameter were not statistically significant; averages were as follows:

D.b.h.	Average	Standard deviation
mm	Percent	
76	36.3	15.6
152	44.1	15.1
228	48.0	13.3

This percentage did, however, have significant positive correlation with latitude, averaging minimum (32.3 percent) at 37.5 degrees and maximum (51.1 percent) at 42.5 degrees (fig. 5-37).

MURRAYANA

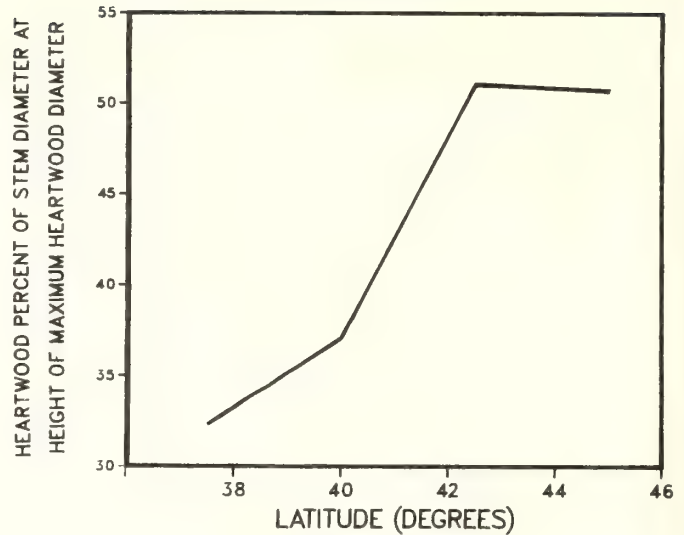


Figure 5-37—Heartwood as percentage of stem diameter at height of maximum heartwood diameter in *murrayana* trees, related to latitude (diameter data pooled).

Heartwood Diameter by Level

Heartwood diameters are negatively correlated with height in tree, but positively correlated with d.b.h. (table 5-2 and figs. 5-38 and 5-39). They are also positively correlated with latitude (fig. 5-39).

Minimum Sapwood Thickness and Location Where Heartwood is Present

Minimum Thickness—Minimum sapwood thickness averaged 29.4 mm, with standard deviation of 10.4 mm. This minimum thickness was positively correlated with d.b.h., averaging 21.5 (6.5), 30.7 (10.2), and 36.1 (9.0) mm for trees of the three diameter classes.

Height at Which Minimum Sapwood Thickness Occurs, Percent—The percentage of tree height where minimum sapwood thickness occurred was positively correlated with d.b.h., averaging 43.3 (18.8), 54.2 (27.1), and 77.5 (10.6) percent for trees 76, 152, and 228 mm in d.b.h.

Height at Which Minimum Sapwood Thickness Occurs, Meters—Tree height (meters) at this minimum sapwood thickness was also positively correlated with d.b.h., averaging 3.23 (1.85), 7.41 (4.48), and 14.56 (4.47) m for trees of the three diameter classes.

MURRAYANA

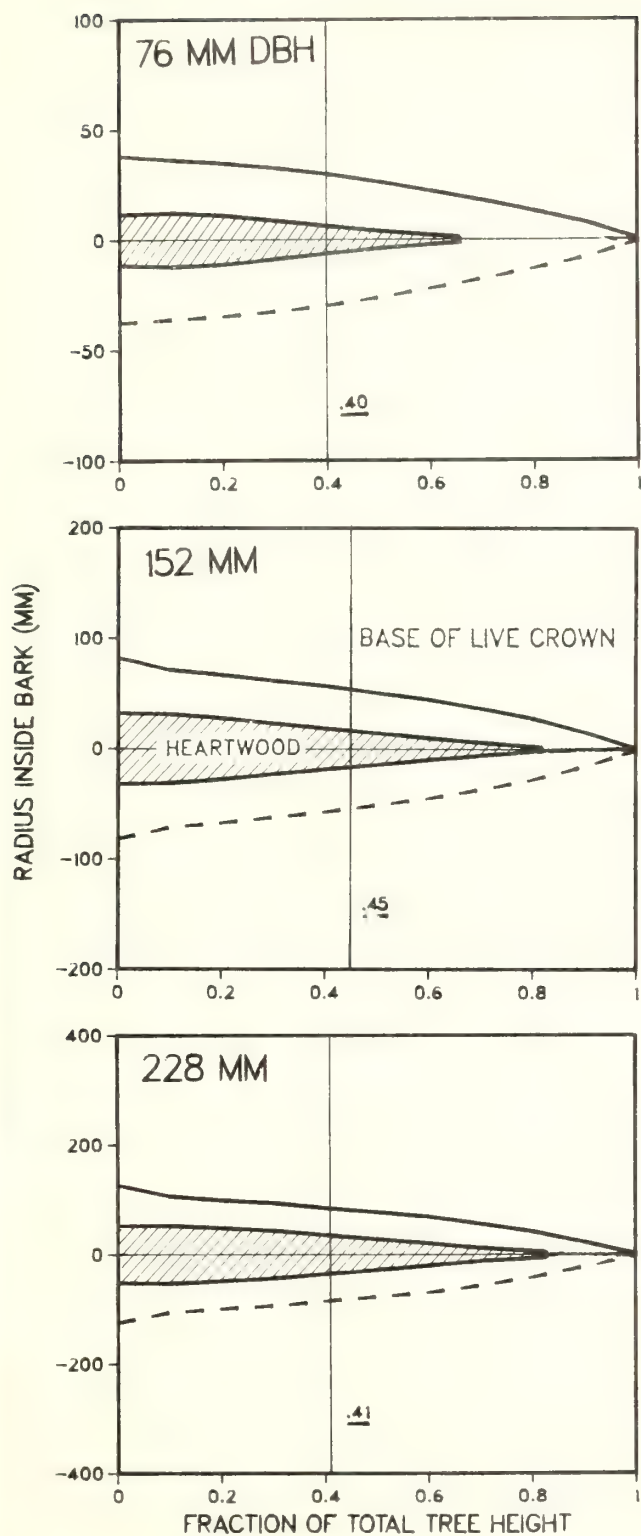


Figure 5-38—Heartwood and stemwood radius in *murrayana* trees of three diameters, related to height in tree and base of live crown.

MURRAYANA

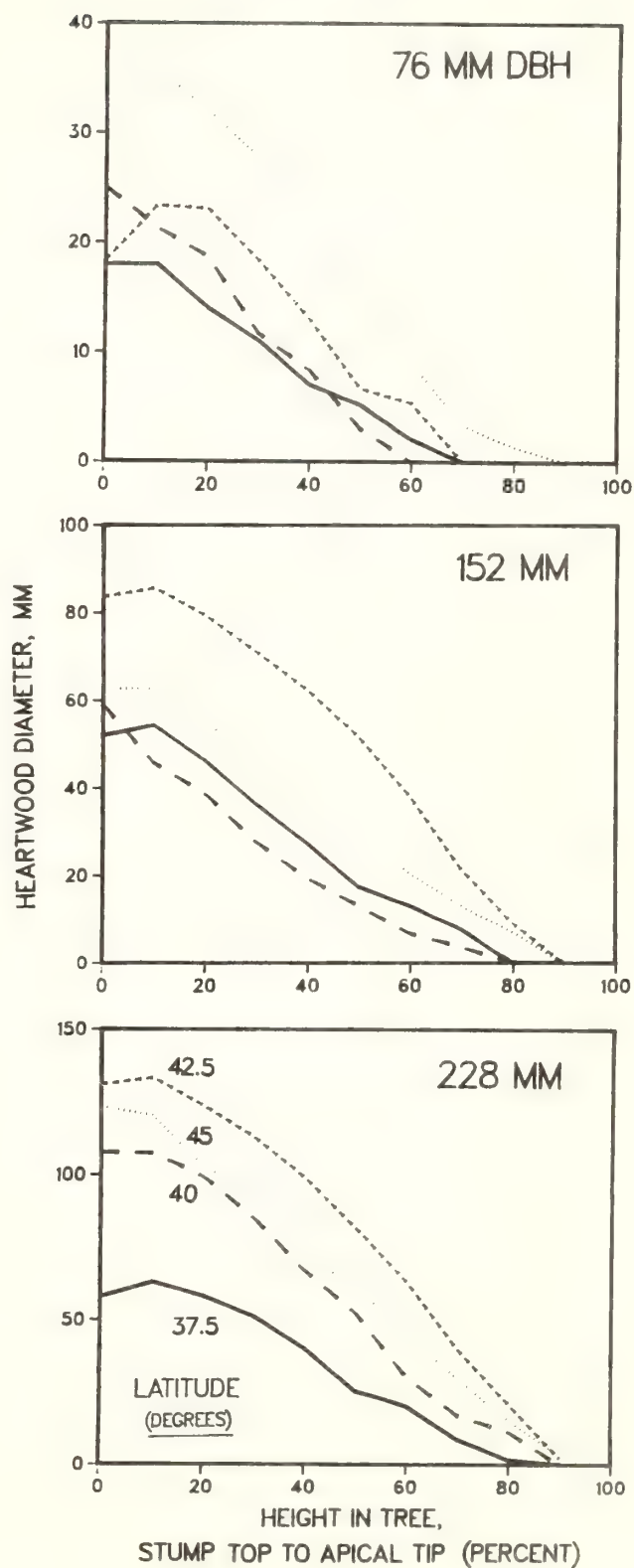


Figure 5-39—Heartwood diameter in *murrayana* trees of three diameters, related to height in tree and latitude.

Sapwood Thickness by Level

Sapwood was thickest at stump height of 152 mm, averaging 26, 50, and 73 mm for trees 76, 152, and 228 mm in d.b.h. It diminished sharply between stump height and 10 percent of tree height, remained more or less constant up to 50 percent of tree height, and then diminished more or less linearly toward the apical tip. Sapwood thickness was positively correlated with d.b.h. at all heights in the tree, but was generally negatively correlated with latitude at levels up to about 70 percent of tree height (fig. 5-40 and table 5-2).

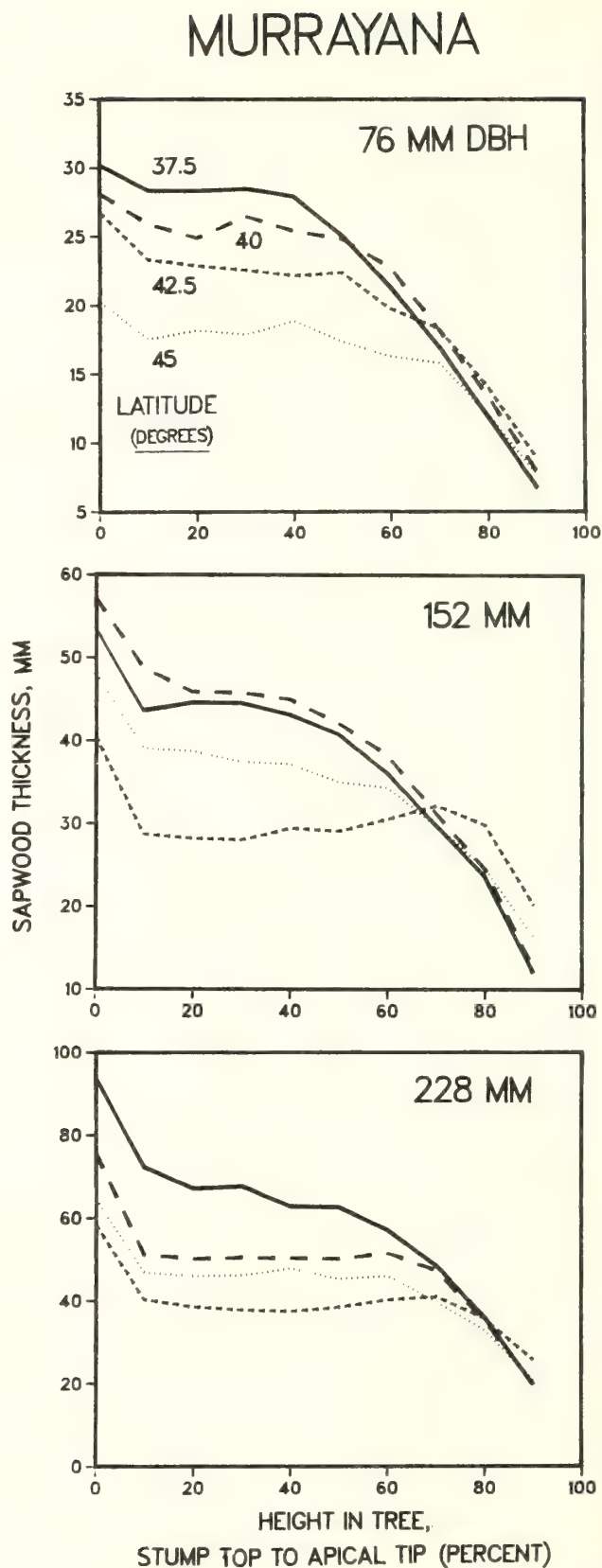


Figure 5-40—Sapwood thickness in *murrayana* trees of three diameters, related to height in tree and latitude.

Heartwood Volume as a Percentage of Entire Stemwood Volume

Heartwood as percentage of stemwood volume was positively correlated with d.b.h., averaging 10.3 (10.7), 16.9 (12.1), and 20.3 (10.5) percent for trees of the three diameter classes. This percentage was also positively correlated with latitude, the average nearly tripling from 37.5 to 45 degrees (fig. 5-41).

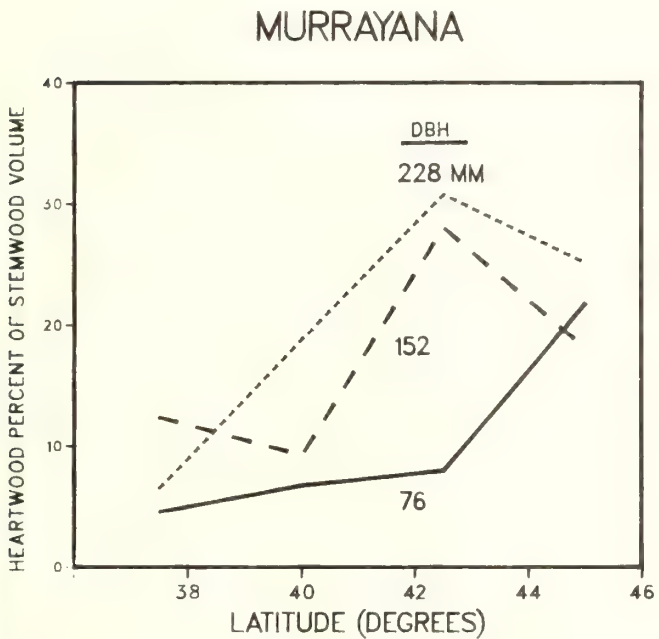


Figure 5-41—Heartwood as percentage of stemwood volume in *murrayana* trees of three diameters, related to latitude.

Heartwood as Percentage of Stemwood Volume by Level

Heartwood as a percentage of stemwood volume averaged about 13, 19, and 20 percent at a stump height of 152 mm for trees 76, 152, and 228 mm in d.b.h.; heartwood percentages were highest (15, 24, and 28 percent, respectively) at 10 percent of tree height, and then decreased more or less linearly toward the apical tip (table 5-2 and fig. 5-42). At all levels in the tree heartwood as percentage of stemwood volume was positively correlated with d.b.h., and was also generally positively correlated with latitude—with large differences among latitudes (fig. 5-42).

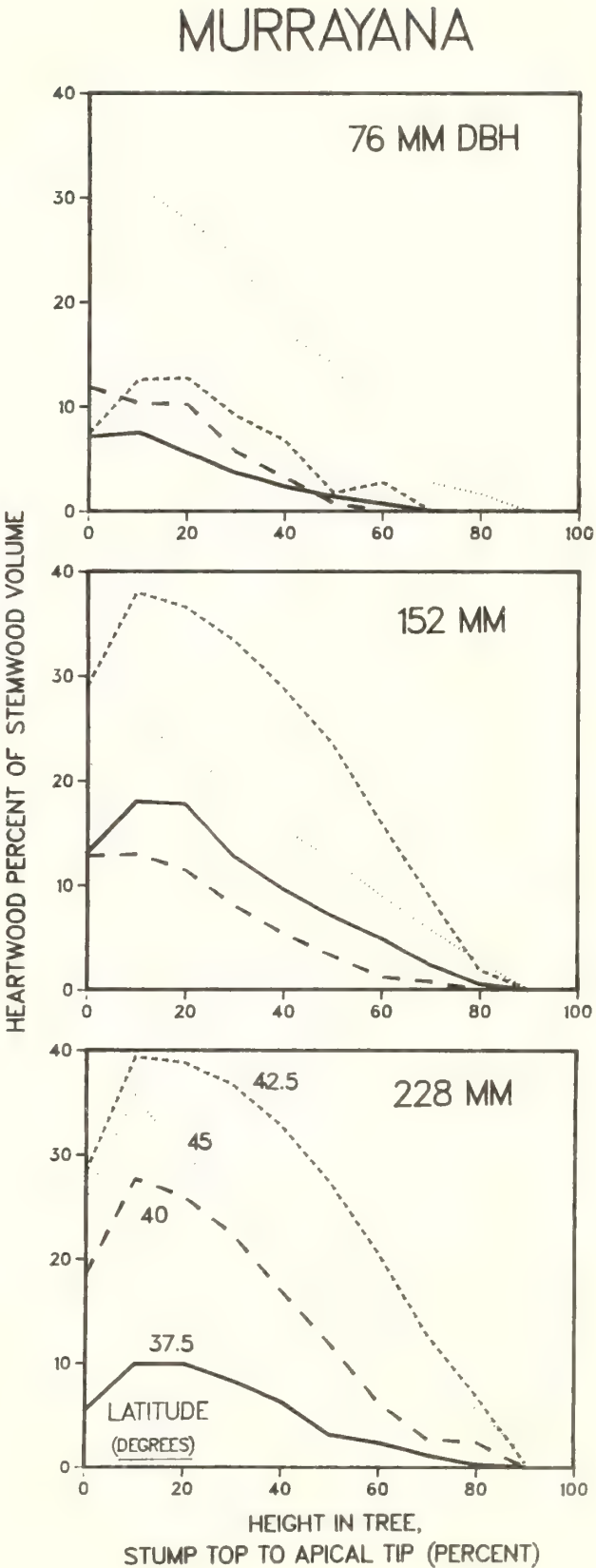


Figure 5-42—Heartwood as percentage of stemwood volume in *murrayana* trees of three diameters, related to height in tree and latitude.

Moisture Content of Entire Stemwood Component

Sapwood—Sapwood moisture content averaged 125.1 percent, with standard deviation of 21.2 percent. Sapwood moisture content was not significantly related to latitude, but had positive significant correlation with diameter, averaging 104.5 (15.5), 128.5 (14.4), and 142.3 (13.3) percent for trees 76, 152, and 228 mm in d.b.h.

Heartwood—The moisture content of entire heartwood averaged 44.4 percent, with standard deviation of 5.8 percent. Moisture content of heartwood was negatively correlated with latitude, averaging 49.0 percent at 37.5 degrees and only 41.1 percent at 45 degrees (fig. 5-43).

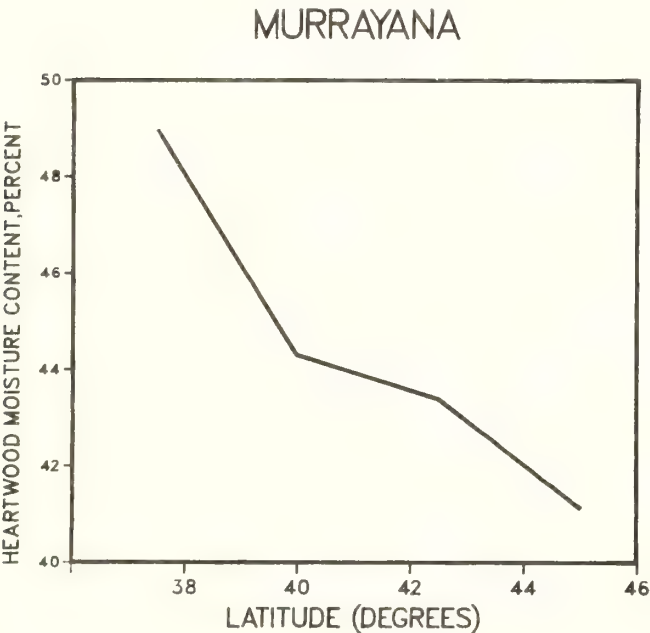


Figure 5-43—Heartwood moisture content in murrayana trees, related to latitude (diameter data pooled).

Although not significantly correlated with diameter, the following tabulation is of interest:

D.b.h.	Average moisture content	Standard deviation
mm	Percent	
76	47.1	6.5
152	43.7	3.0
228	42.6	6.7

Moisture Content of Sapwood by Level

Moisture content of sapwood increased more or less linearly from stump height to about 80 percent of tree height and was positively correlated with d.b.h. at all heights (table 5-2 and fig. 5-44).

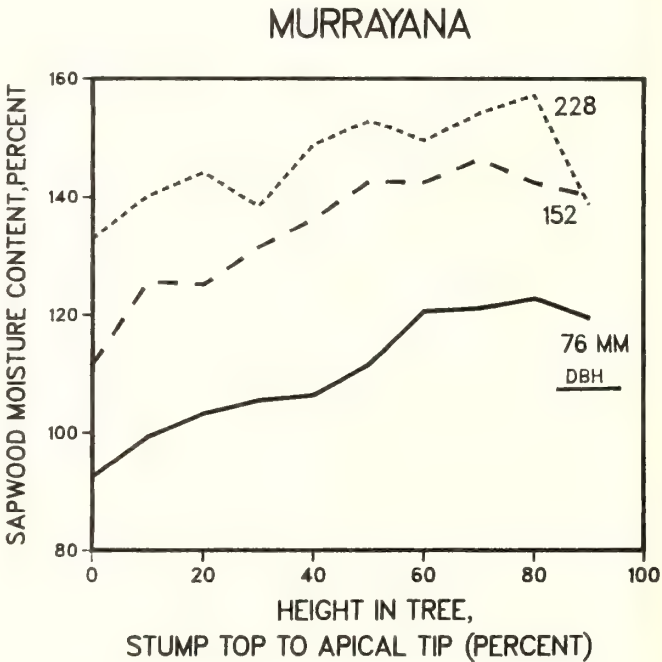


Figure 5-44—Sapwood moisture content in murrayana trees of three diameters, related to height in tree.

Moisture Content of Heartwood by Level

Moisture content of heartwood, although positively correlated with height in stem, varied much less with height than moisture content of sapwood (table 5-2 and fig. 5-45). Heartwood moisture content was inversely correlated with latitude at most heights (fig. 5-45).

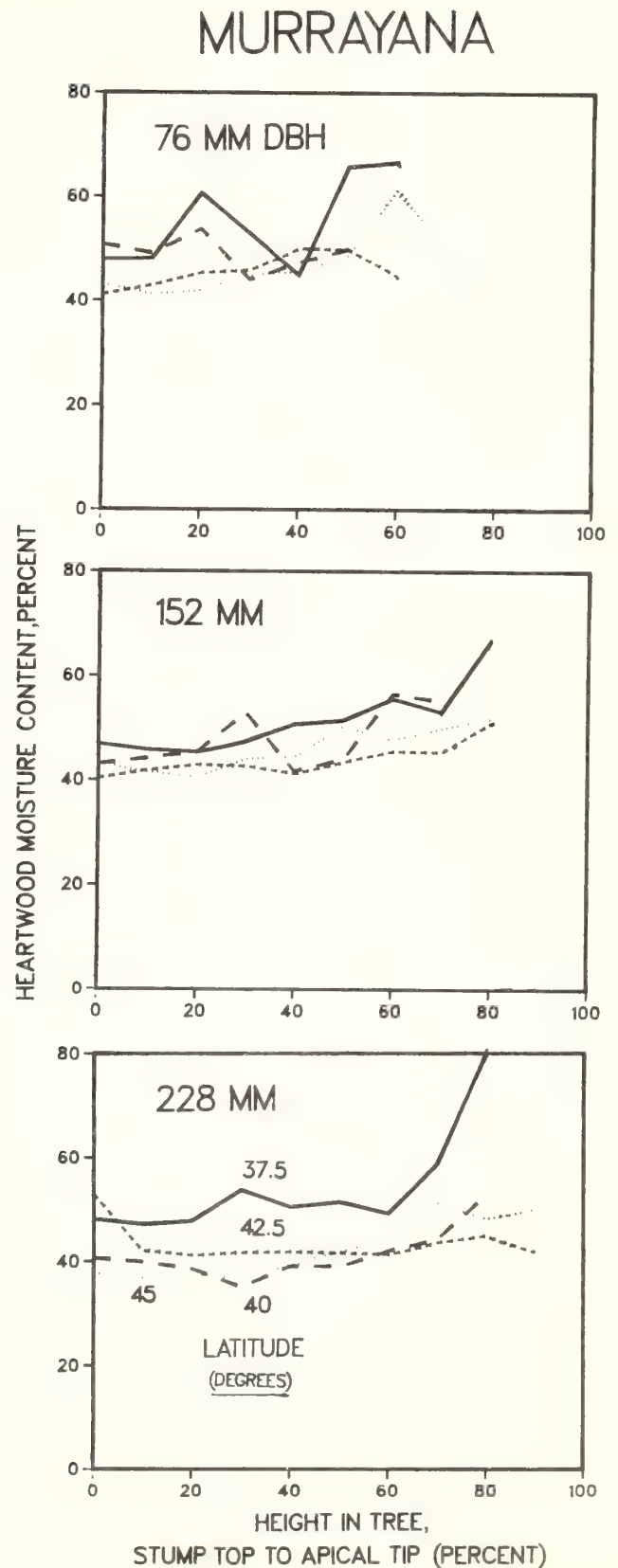


Figure 5-45—Heartwood moisture content in *murrayana* trees of three diameters, related to height in tree and latitude.

Weight of Sapwood in Entire Stem

Green—Green sapwood weight was positively correlated with d.b.h., averaging 13.60 (3.48), 88.54 (25.48), and 253.53 (60.56) kg for trees of the three diameter classes. Green sapwood weight was not significantly correlated to latitude; values were as follows:

Latitude	76 mm	152 mm	228 mm
Degrees	----- Kilograms -----		
37.5	12.74	61.18	238.41
40	13.85	89.66	256.80
42.5	13.97	103.02	260.12
45	13.83	100.29	258.78

Ovendry—Similarly, sapwood ovendry weight was positively correlated with diameter, averaging 6.74 (1.75), 39.00 (11.72), and 105.30 (26.76) kg for trees 76, 152, and 228 mm in d.b.h. Ovendry weights of sapwood were not significantly correlated with latitude; values were as follows:

Latitude	76 mm	152 mm	228 mm
Degrees	----- Kilograms -----		
37.5	6.32	26.29	92.71
40	7.12	38.74	105.80
42.5	6.51	45.06	109.69
45	7.01	45.91	113.01

Weight of Heartwood in Entire Stem

Green—It was noted in chapter 4 that although heartwood specific gravity averaged least at 42.5 degrees latitude, weight of green heartwood was greatest at this latitude (fig. 4-124, top). Heartwood green weight was positively correlated with d.b.h. at all latitudes, averaging 1.38 (1.42), 14.88 (12.87), and 45.28 (29.60) kg for trees of the three diameter classes.

Ovendry—On an ovendry-weight basis, latitudinal and diameter trends were similar (fig. 4-124, bottom), with heartwood weights for trees of the three diameter classes averaging 0.95 (0.99), 10.46 (9.10), and 32.25 (21.55) kg. From the large standard deviations in dry heartwood weight it is evident that trees varied greatly in their heartwood content.

Heartwood as Percentage of Weight of Entire Stemwood

Green—Green heartwood weight as percentage of entire green stemwood averaged 6.2, 9.0, 16.2, and 16.6 percent at latitudes 37.5, 40, 42.5, and 45 degrees (diameter data pooled), and was generally positively correlated with diameter, averaging 8.8 (9.6), 12.9 (9.2), and 14.3 (7.3) percent for trees 76, 152, and 228 mm in d.b.h. (fig. 5-46).

Ovendry—Heartwood ovendry weight percent of stemwood averaged least (9.2 percent) at 37.5 degrees and most (23.2 percent) at 42.5 degrees latitude (fig. 4-125). The percentage was positively correlated with d.b.h., averaging 11.4 (11.1), 18.3 (11.9), and 21.5 (10.0) percent for trees of the three diameter classes.

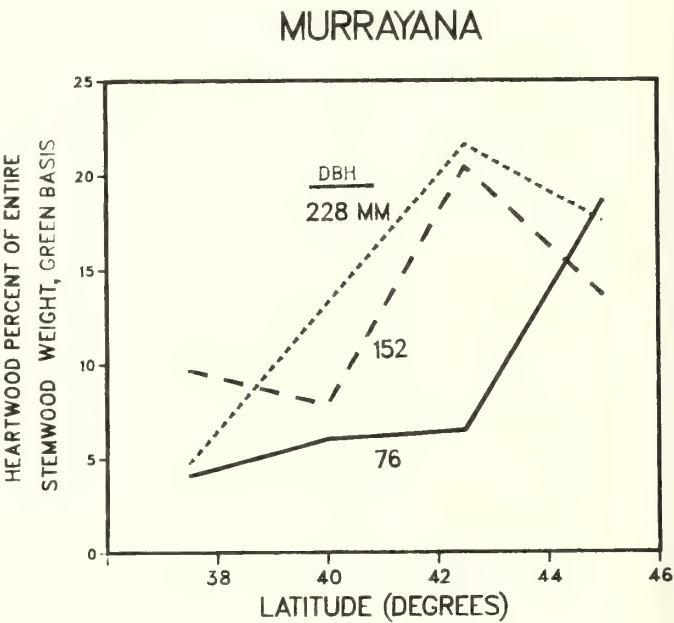


Figure 5-46—Green heartwood as percentage of entire green stemwood weight of murrayana trees of three diameters, related to latitude.

Heartwood as Percentage of Stemwood Weight by Level

Green—At most heights in the tree, heartwood as percentage of green stemwood weight was unrelated to d.b.h., but was positively correlated with latitude; at 10 percent of tree height, heartwood as percentage of green weight averaged 9.4 percent at 37.5 degrees and 24.2 percent at 45 degrees. With diameter and latitudinal data pooled, it averaged 14.1 percent at stump height of 152 mm, increased to 17.4 percent at 10 percent of tree height, and then decreased toward the apical tip (fig. 5-47 and table 5-2).

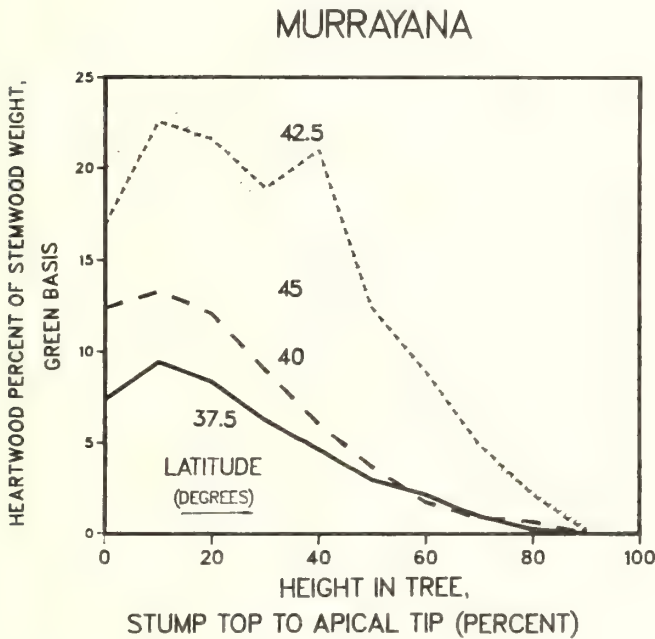


Figure 5-47—Green heartwood as percentage of green stemwood weight of *murrayana* trees of three diameters, related to height in tree and latitude.

Ovendry—On an ovendry weight basis, both d.b.h. and latitude were significant factors related to variation with height of heartwood as a percentage of stemwood weight (fig. 5-48). At all heights in the trees, heartwood ovendry weight as a percentage of stemwood was positively correlated with d.b.h., and at all levels, trees from latitudes 37.5 and 40 degrees had a lower percentage of heartwood in terms of ovendry-weight than those from latitudes 42.5 and 45 degrees. With latitudinal data pooled, heartwood ovendry weight as a percentage of stemwood averaged as follows (fig. 5-48 and table 5-2):

D.b.h.	Stump height of 152 mm	10 percent height	80 percent height
mm		Percent	
76	14.3	16.8	0.4
152	20.7	25.0	1.5
228	21.6	29.4	4.4

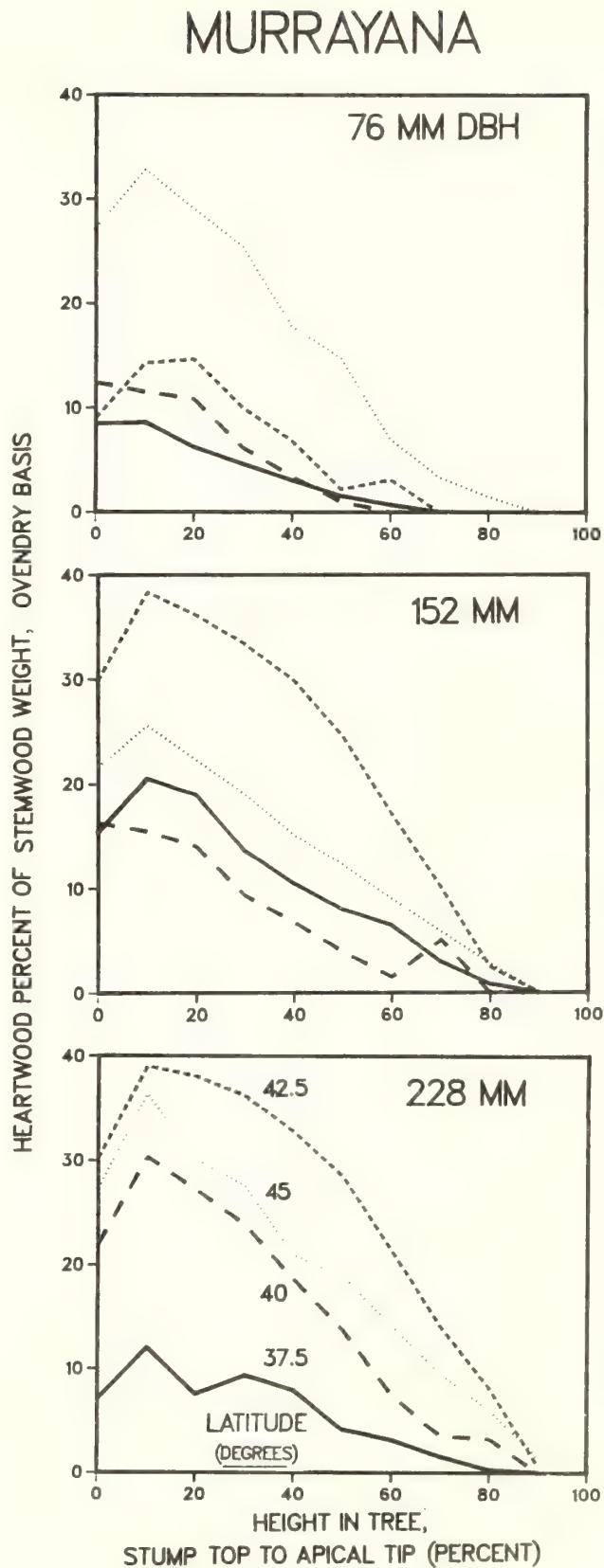


Figure 5-48—Ovendry heartwood as percentage of ovendry stemwood weight of *murrayana* trees of three diameters, related to height in tree and latitude.

Specific Gravity of Sapwood in Entire Stem

As noted in chapter 4, sapwood specific gravity of the 152- and 228-mm trees (based on green volume and unextracted oven-dry weight) averaged significantly less in the south than in the north (fig. 4-123, top). Also, sapwood specific gravity was negatively correlated with d.b.h., averaging 0.476 (0.038), 0.433 (0.044), and 0.401 (0.032) for trees 76, 152, and 228 mm in d.b.h. Overall average was 0.437 with standard deviation of 0.048.

Specific Gravity of Sapwood by Level

At all heights in the trees, specific gravity of sapwood was inversely correlated with d.b.h. (fig. 5-49 and table 5-2). With all data pooled, specific gravity averaged greatest at stump height of 152 mm (0.479), and least at about 70 percent of tree height (0.408). In general, sapwood specific gravity variation with height was unrelated to latitude.

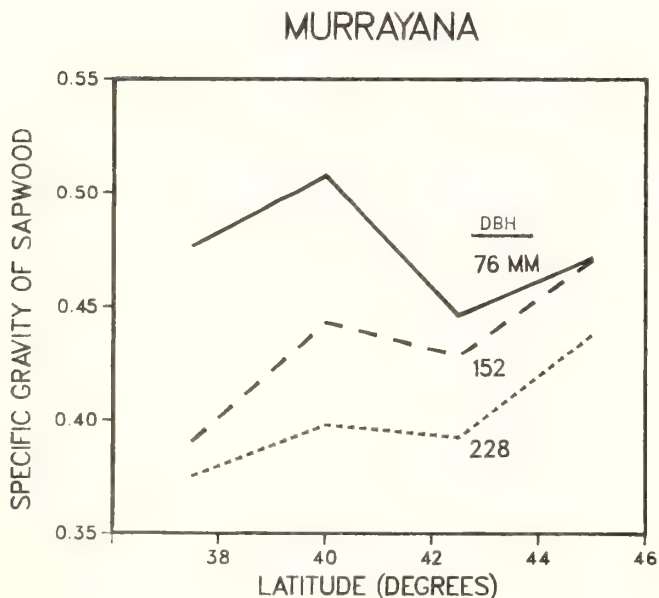


Figure 5-49—Specific gravity of sapwood (based on green volume and unextracted oven-dry weight) of *murrayana* trees of three diameters, related to height in tree.

MURRAYANA

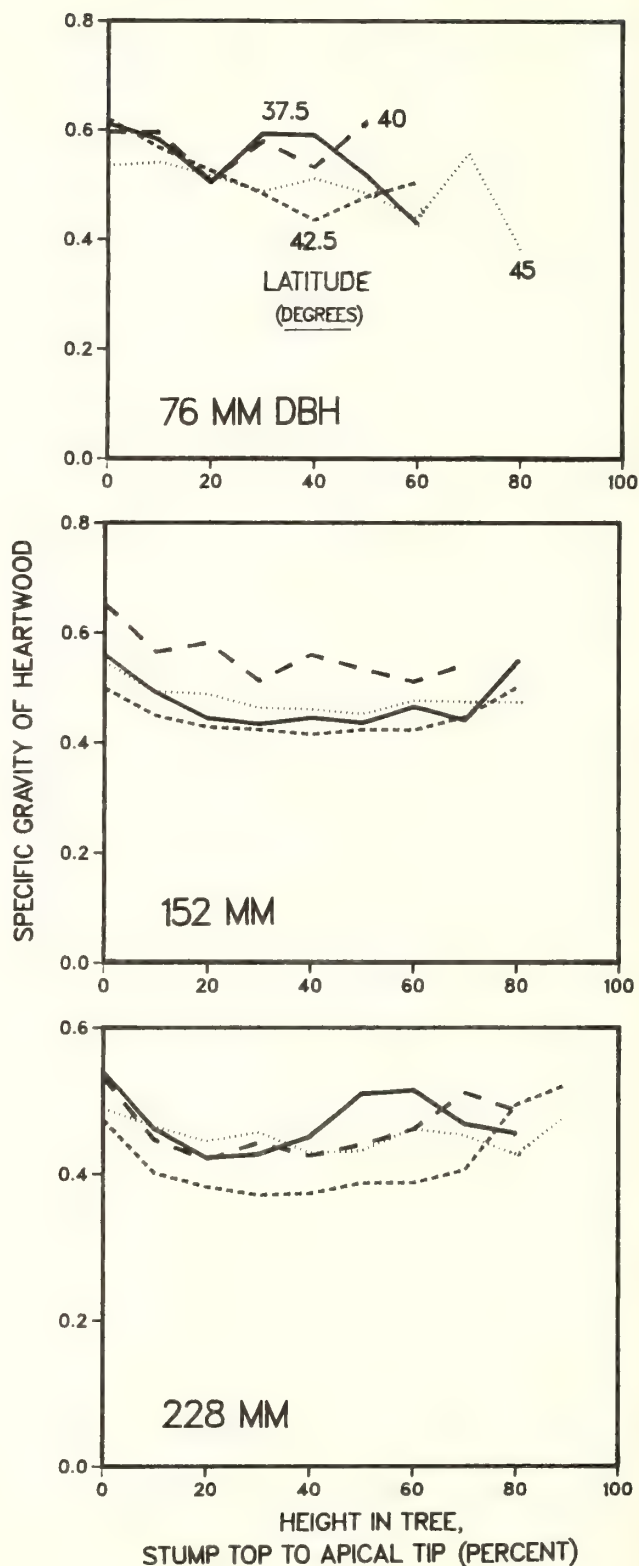


Figure 5-50—Specific gravity of heartwood (based on green volume and unextracted oven-dry weight) of *murrayana* trees of three diameters, related to height in tree and latitude.

Specific Gravity of Heartwood in Entire Stem

As noted in chapter 4, heartwood specific gravity, based on green volume and unextracted oven-dry weight, averaged maximum (0.547) at 40 degrees and minimum (0.461) at 42.5 degrees (fig. 4-123, bottom). It was negatively correlated with diameter, averaging 0.550 (0.046), 0.508 (0.071), and 0.446 (0.037) for trees 76, 152, and 228 mm in d.b.h. With all data pooled, heartwood specific gravity was greater than that of sapwood (probably because of a higher content of extractives), and averaged 0.502, with standard deviation of 0.067.

Specific Gravity of Heartwood by Level

Heartwood specific gravity varied less than that of sapwood with height in tree (figs. 5-49 and 5-50); it was maximum at stump height of 152 mm where it averaged 0.555, and averaged minimum at 40 percent of tree height (0.461). In general, heartwood specific gravity at all heights was minimum at 42.5 degrees latitude (fig. 5-50). At all heights except 60 and 80 percent, heartwood specific gravity was inversely correlated with d.b.h. (table 5-2).

5-7 RESULTS—*LATIFOLIA* COMPARED TO *MURRAYANA* WITHIN LATITUDINAL SAMPLING ZONES OF 40, 42.5, AND 45 DEGREES

The following comparisons between varieties are limited to the three latitudinal sampling zones they have in common, namely 40, 42.5, and 45 degrees.

Height Where Maximum Heartwood Diameter Occurs

Proportion—In *latifolia*, maximum heartwood diameter occurred at an average of 8.5 percent of tree height; it averaged lower in *murrayana* (6.3 percent), but the relationship varied with both d.b.h. and latitude (fig. 5-51).

COMPARISON

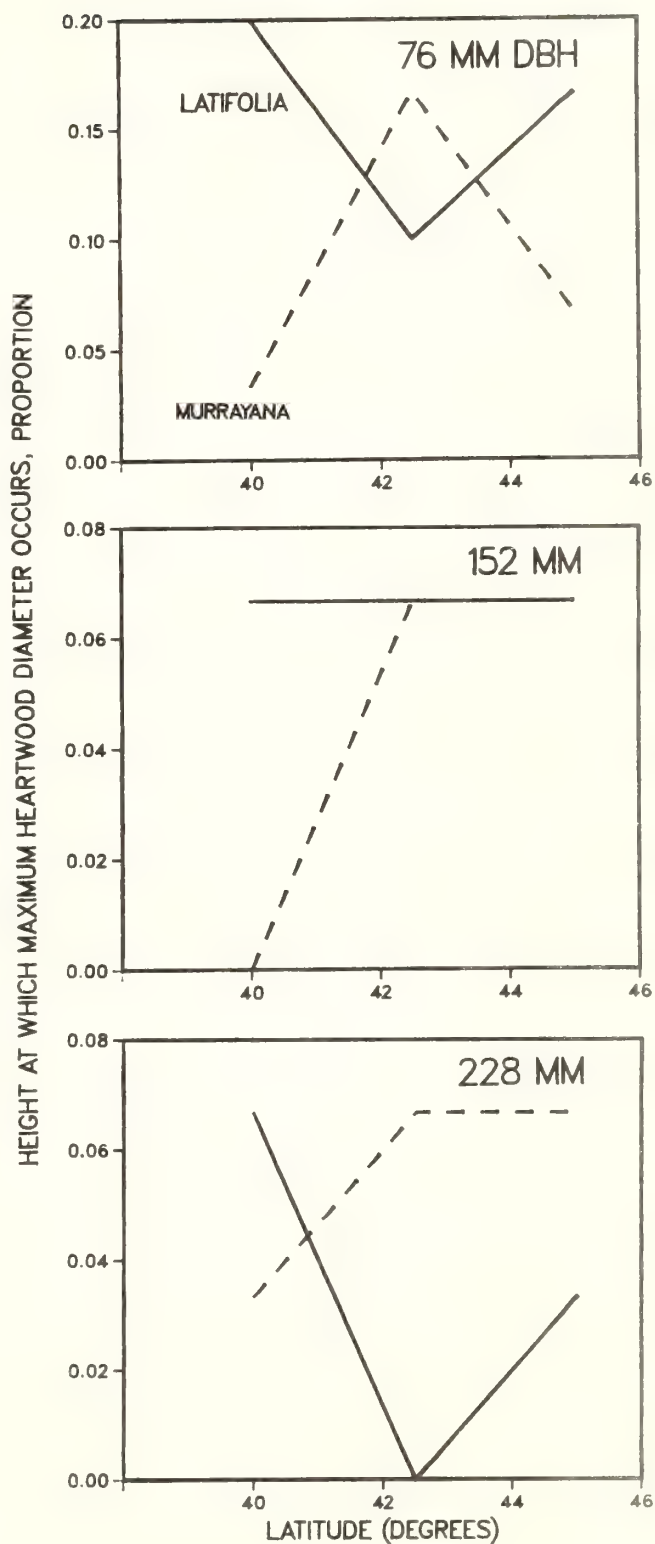


Figure 5-51—Proportion of height at which maximum heartwood diameter occurs in *latifolia* and *murrayana* trees of three diameters, related to latitude.

Meters—In *latifolia*, maximum heartwood diameter occurred at an average height of 1.01 m above stump top, while in *murrayana*, the average was 0.81 m, but the relationship varied with d.b.h. and latitude (fig. 5-52).

Heartwood Volume as Percentage of Stemwood Volume

Although varietal differences were not statistically significant, the following heartwood volumes as percentages of stemwood volumes (averaged for the three latitudinal zones they have in common) are of interest:

D.b.h.	<i>Latifolia</i>	<i>Murrayana</i>
mm	-----	Percent -----
76	14.8	12.2
152	21.4	18.4
228	30.1	24.9

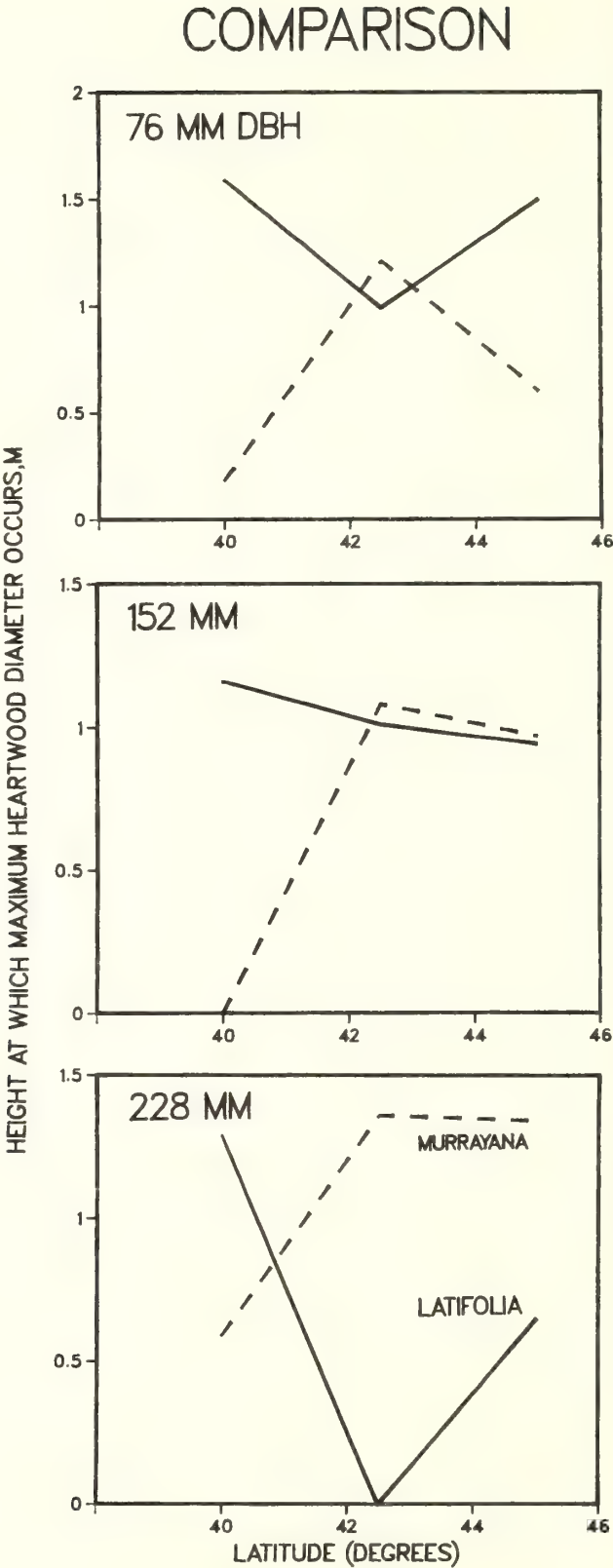


Figure 5-52—Height (meters) at which maximum heartwood diameter occurs in *latifolia* and *murrayana* trees of three diameters, related to latitude.

Specific Gravity of Sapwood

Specific gravity of entire sapwood, based on green volume and unextracted oven-dry weight, averaged significantly greater in *murrayana* (0.444) than in *latifolia* (0.397); this relationship occurred in all three diameter classes (fig. 5-53).

At all heights in the trees *murrayana* had greater sapwood specific gravity than *latifolia* (fig. 5-54).

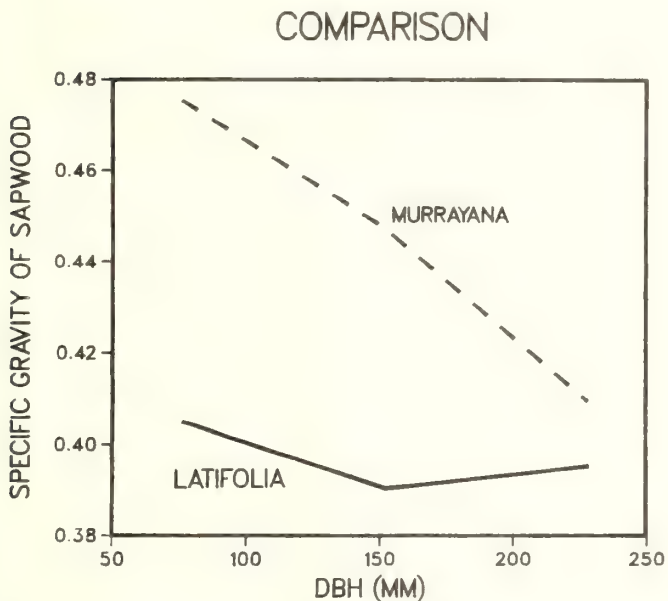


Figure 5-53—Specific gravity of sapwood of *latifolia* and *murrayana* trees related to d.b.h.; data from latitudes 40, 42.5, and 45 degrees pooled.

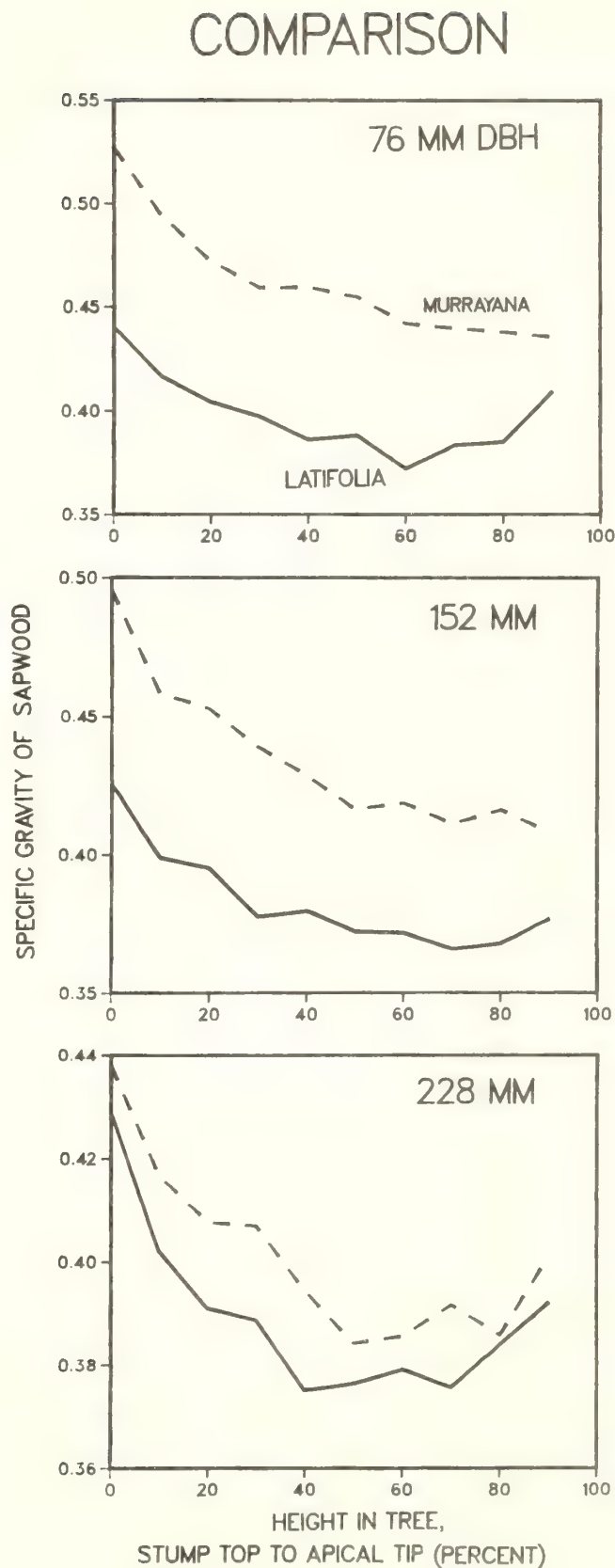


Figure 5-54—Specific gravity of sapwood of *latifolia* and *murrayana* trees of three diameters related to height in tree; data from latitudes 40, 42.5, and 45 degrees pooled.

COMPARISON

Specific Gravity of Heartwood

Specific gravity of entire heartwood, based on green volume and unextracted oven-dry weight, also averaged significantly higher in *murrayana* (0.500) than in *latifolia* (0.427); this relationship occurred at all three latitudes and in all three diameter classes (fig. 5-55).

At all heights in the trees (except 80 percent in 76-mm trees), heartwood specific gravity of *murrayana* significantly exceeded that of *latifolia* (fig. 5-56).

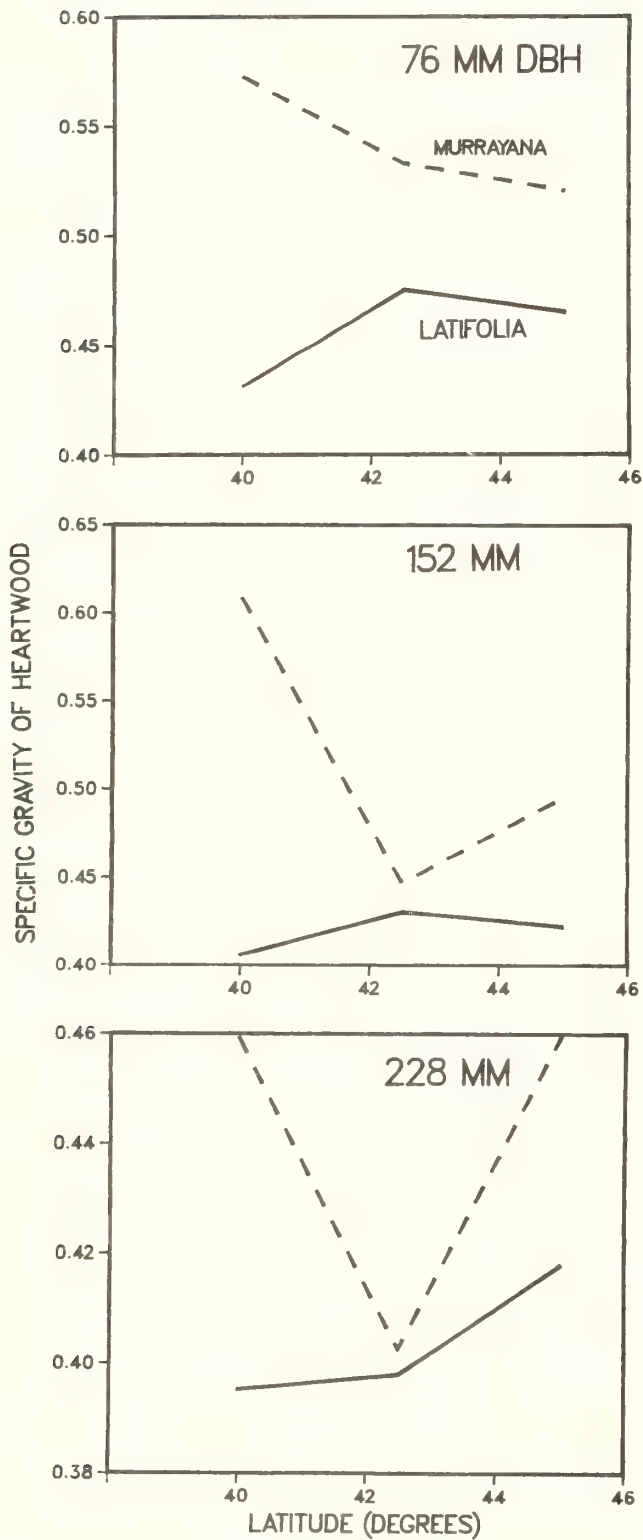


Figure 5-55—Specific gravity of heartwood of *latifolia* and *murrayana* trees of three diameters, related to latitude.

COMPARISON

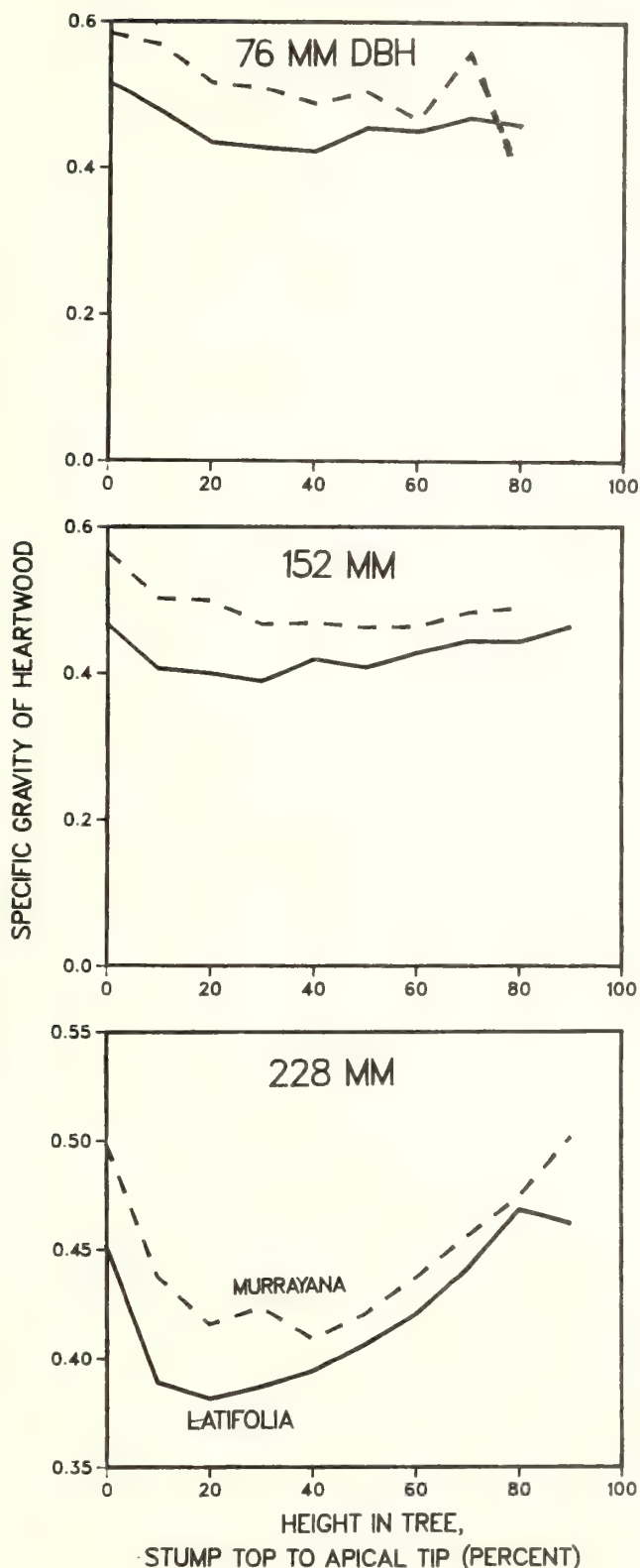


Figure 5-56—Specific gravity of heartwood of *latifolia* and *murrayana* trees of three diameters related to height in tree; data from latitudes 40, 42.5, and 45 degrees pooled.

5-8 SUMMARY OF RESULTS

In *latifolia*, the age of the lowest tree disk where heartwood did not occur averaged 21, 11, and 10 years in trees 76, 152, and 228 mm in d.b.h.; this age was also negatively correlated with latitude. The height of this lowest heartwood-free disk averaged 76, 90, and 94 percent in trees of the three diameters, and was positively correlated with latitude.

The height (above a stump height of 152 mm) in *latifolia* at which maximum heartwood diameter occurred averaged 0.80, 0.53, and 0.44 m for trees 76, 152, and 228 mm in d.b.h.; this height was also negatively correlated with latitude. Heartwood as percentage of stem diameter at height of maximum heartwood diameter was positively correlated with latitude, and averaged 48, 54, and 60 percent for trees of the three diameter classes.

In *latifolia*, minimum sapwood thickness where heartwood was present averaged 16, 24, and 29 mm for trees 76, 152, and 228 mm in d.b.h.; trees in northern latitudes and middle- to upper-elevation zones (within latitudinal zones) had thinnest sapwood. This minimum sapwood thickness occurred at 51, 60, and 70 percent of height in trees of the three diameter classes; the percent height was positively correlated with latitude. Sapwood thickness was maximum near ground level, diminished rapidly up to about 10 percent of tree height, remained more or less constant to about 70 percent of tree height, and finally diminished with approach to the apical tip. Sapwood was thinnest in northern latitudes.

Heartwood volume as a percentage of entire stemwood volume in *latifolia* averaged 22, 28, and 34 percent in trees 76, 152, and 228 mm in d.b.h.; heartwood volume percentages were positively correlated with latitude.

Sapwood moisture content in *latifolia* averaged 119 percent, with moisture contents of 110, 122, and 126 percent in trees 76, 152, and 228 mm in d.b.h.; it was negatively correlated with latitude. Sapwood moisture content was minimum in the lowest 10 percent of the stems (110 percent), increased more or less linearly to a maximum (136 percent) at about 80 percent of tree height, and then diminished slightly toward the apical tip.

Heartwood moisture content in *latifolia* averaged 43 percent, with moisture contents of 47, 42, and 41 percent in trees 76, 152, and 228 mm in d.b.h. Average heartwood moisture content was lowest (42 percent) at stump height of 152 mm and increased curvilinearly to a maximum (52 percent) at 90 percent of tree height.

Heartwood as a percentage of oven-dry weight of entire *latifolia* stemwood averaged 23, 29, and 35 percent for trees 76, 152, and 228 mm in d.b.h.; these percentages were positively correlated with latitude.

Specific gravity of sapwood in entire stems (based on green volume and unextracted oven-dry weight) averaged 0.414, and was maximum at middle latitudes; it was 0.423, 0.415, and 0.405 in trees 76, 152, and 228 mm in d.b.h. Sapwood specific gravity averaged 0.449 at stump height, decreased to a minimum of 0.387 at 70 percent of tree height, and then increased to 0.399 at 90 percent of tree height.

Specific gravity of heartwood of entire *latifolia* stemwood averaged 0.434; it was 0.459, 0.430, and 0.412 in

trees 76, 152, and 228 mm in d.b.h. With diameter data pooled, heartwood had average specific gravity of 0.482 at stump height of 152 mm, decreased sharply to a minimum of 0.412 at 30 percent of tree height, and then increased to a near maximum (0.478) at 90 percent.

In the three latitudinal sampling zones common to the two varieties (40, 42.5, and 45 degrees), some significant differences were observed between *latifolia* and *murrayana*. In *latifolia*, maximum heartwood diameter occurred at an average of 8.5 percent of tree height (1.01 m above stump top); it averaged lower in *murrayana* (6.3 percent and 0.81 m). Specific gravity of entire sapwood averaged significantly higher in *murrayana* (0.444) than in *latifolia* (0.397); at all heights in trees, *murrayana* had greater sapwood specific gravity than *latifolia*. Specific gravity of heartwood also averaged significantly higher in *murrayana* (0.500) than in *latifolia* (0.427); this relationship applied to all latitudes, diameters, and heights in trees.

5-9 REFERENCES

- Alexander, J. B. The strength of lodgepole pine telephone poles. Forest Service Circular 42. Ottawa, ON: Department of the Interior, Canada, Forest Service, Forest Products Laboratories; 1934. 14 p.
- Anderson, Arthur B.; Riffer, Richard; Wong, Addie. Monoterpenes, fatty and resin acids of *Pinus contorta* and *Pinus attenuata*. *Phytochemistry*. 8(12): 2401-2403; 1969.
- Ballard, R. G.; Walsh, M. A.; Cole, W. E. The penetration and growth of blue-stain fungi in the sapwood of lodgepole pine attacked by mountain pine beetle. *Canadian Journal of Botany*. 62(8): 1724-1729; 1984.
- Bouchier, R. J. Laboratory studies on microfungi isolated from the stems of living lodgepole pine, *Pinus contorta* Dougl. *Canadian Journal of Botany*. 39(6): 1373-1385; 1961a.
- Bouchier, R. J. Two new imperfect fungi from the heartwood of living lodgepole pine. *Canadian Journal of Botany*. 39(7): 1781-1784; 1961b.
- Brazier, J. D. A report on the effects of provenance on the timber properties of lodgepole pine. In: *Pinus contorta* as an exotic species: proceedings, IUFRO working party meeting on *Pinus contorta* provenances (S2-02-06) in Norway and Sweden. Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics; 1980: 181-207.
- Cooper, P. A. Effect of species, precompression, and seasoning on heartwood preservative treatability of six western conifers. *Forest Products Journal*. 23(7): 51-59; 1973.
- Cooper, P. A.; Bramhall, G.; Ross, N. A. Estimating preservative treatability of wood from its air-flow properties. *Forest Products Journal*. 24(9): 99-103; 1974.
- Denyer, W. B. G. Red stain in lodgepole pine in Alberta. Bi-monthly Progress Report. 8(2): 3-4; 1952.
- Eades, H. W.; Roff, J. W. Red heart stain of lodgepole pine logs in the northern interior of British Columbia. V-1023. Vancouver, BC: Department of Northern Affairs and National Resources, Forestry Branch, Forest Products Laboratories of Canada, Vancouver Laboratory; 1957. 14 p.
- Eades, H. W.; Roff, J. W. Red heart stain of lodgepole pine logs in the southern interior of British Columbia. V-1025. Vancouver, BC: Department of Northern Affairs and National Resources, Forestry Branch, Forest Products Laboratories of Canada, Vancouver Laboratory; 1959. 11 p.
- Englerth, George H.; Scheffer, Theodore S. Tests of decay resistance of four western pole species. *Journal of Forestry*. 53(8): 556-561; 1955.
- Erdtman, Holger. Heartwood extractives of conifers. *Tappi*. 32(7): 305-310; 1949.
- Eslyn, W.-E. Utility pole decay, part 3: detection in pine by color indicators. *Wood Science Technology*. 13: 117-126; 1979.
- Fosberg, Michael A. Drying rates of heartwood below fiber saturation. *Forest Science*. 16(1): 57-63; 1970.
- Graham, R. D. The preservative treatment of eight Oregon conifers by pressure processes. *Proceedings of the American Wood-Preservation Association*. 52: 118-139; 1956.
- Hakkila, Pentti; Panhelainen, Arja. On the wood properties of *Pinus contorta* in Finland. *Communications Instituti Forestalis Fenniae*. 73(1): 1970. 43 p.
- Harris, J. Maddern. The use of beta rays in determining wood properties—part 5: measuring resin content. *New Zealand Journal of Science*. 12(2): 443-451; 1969.
- Harris, J. Maddern. Physical properties, resin content, and tracheid length of lodgepole pine grown in New Zealand. *New Zealand Journal of Forest Science*. 3(1): 91-109; 1973.
- Kaufmann, Merrill R.; Troendle, Charles A. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *Forest Science*. 27(3): 477-482; 1981.
- Lassen, L. E.; Okkonen, E. A. Sapwood thickness of Douglas-fir and five other western softwoods. Research Paper FPL 124. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory; 1969. 16 p.
- Lieu, Peter J.; Kelsey, Rick G.; Shafizadeh, Fred. Some chemical characteristics of green and dead lodgepole pine and western white pine. Research Note INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 8 p.
- Lindstedt, Gösta. Constituents of pine heartwood: IX. The heartwood of *Pinus montana* Mill. X. The heartwood of *Pinus contorta* var. *latifolia* S. Wats. XI. The heartwood of *Pinus radiata* D. Don. XII. The heartwood of *Pinus ponderosa* Dougl. XIII. The heartwood of *Pinus jeffreyi* Balf. *Acta Chem. Scand*. 3(7): 755-772; 1949.
- Loman, A. A. The effect of heartwood fungi of lodgepole on its phenolic heartwood extractives. In: Shigo, Alex L., chairman. Interaction of organisms in the process of decay of forest trees: symposium. Bulletin 13. Quebec, Canada: Laval University Research Foundation; 1970a: 39-43.
- Loman, A. A. The effect of heartwood fungi of *Pinus contorta* var. *latifolia* on pinosylvins, pinosylvinmonomethyl

- ether, pinobanksin, and pinocembrin. *Canadian Journal of Botany*. 48: 737-747; 1970b.
- Loman, A. A.; Paul, G. D. Decay of lodgepole pine in two foothills sections of the Boreal Forest in Alberta. *Forestry Chronicle*. 39(4): 422-435; 1963.
- Lopushinsky, William. Water relations and photosynthesis in lodgepole pine. In: Baumgartner, David M., ed. *Management of lodgepole pine ecosystems: symposium proceedings*; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service, College of Agriculture; 1975: 135-153. (vol. 1).
- Lowery, David P.; Rasmussen, E. F. Accelerated drying of lodgepole pine and western larch poles. *Forest Products Journal*. 13(6): 221-226; 1965.
- Markstrom, Donald C.; Hann, Robert A. Seasonal variation in wood permeability and stem moisture content of three Rocky Mountain softwoods. Research Note RM-212. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1972. 7 p.
- Markstrom, Donald C.; Mueller, Lincoln A.; Gjovik, Lee R. Treating resistant Rocky Mountain species by regular and modified double-diffusion methods. *Forest Products Journal*. 20(12): 17-20; 1970.
- Meyer, R. W. Effect of enzyme treatment on bordered-pit ultrastructure, permeability, and toughness of the sapwood of three western conifers. *Wood Science*. 6(3): 220-230; 1974.
- Owston, Peyton W.; Smith, James L.; Halverson, Howard G. Seasonal water movement in tree stems. *Forest Science*. 18(4): 266-272; 1972.
- Pearson, John Allan. Biomass distribution and ecosystem development in lodgepole pine forests of the Medicine Bow Mountains, Wyoming. Laramie, WY: University of Wyoming; 1982. 113 p. Ph.D. dissertation.
- Reid, R. W. Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. *Forestry Chronicle*. 37(4): 368-375, 403; 1961.
- Rickey, R. G.; Hergert, H. L. Reactions in pine heartwood during acid bisulfite pulping. *Tappi*. 57(7): 114-117; 1974.
- Ruddick, John N. R. Treatability of lodgepole pine lumber with ACA and CCA. *Forest Products Journal*. 30(2): 28-32; 1980.
- Running, Steven W. Relating plant capacitance to the water relations of *Pinus contorta*. *Forest Ecology and Management*. 2(4): 237-252; 1980.
- Shrimpton, D. M. Variations in the extractives from lodgepole pine sapwood and heartwood. Information Report NOR-X-18. Edmonton, AB: Department of the Environment, Canadian Forestry Service, Northern Forest Research Centre; 1972. 22 p.
- Shrimpton, D. M. Extractives associated with wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. *Canadian Journal of Botany*. 51(3): 527-534; 1973.
- Sylvander, Robert B.; Smith, J. Harry G. Widths and specific gravity of earlywood and latewood components of annual rings from interior British Columbia lodgepole pine. Vancouver, BC: University of British Columbia, Faculty of Forestry; 1973. 61 p.
- Thompson, Dan C. Sapwood-leaf area relations in lodgepole pine in western Montana. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. *Lodgepole pine: the species and its management: symposium proceedings*; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 380. Abstract.
- Waring, R. H.; Schroeder, P. E.; Oren, R. Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research*. 12(3): 556-560; 1982.
- Yang, Kung-Chi. Sapwood thickness in *Pinus contorta* Dougl. ex Loud. In: Baumgartner, David M.; Krebill, Richard G.; Arnott, James T.; Weetman, Gordon F., eds. *Lodgepole pine: the species and its management: symposium proceedings*; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 380. Abstract.

Koch, Peter. 1987. Gross characteristics of lodgepole pine trees in North America. Gen. Tech. Rep. INT-227. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 311 p.

Presents gross characteristics of North American lodgepole pine (*Pinus contorta*) as an industrial raw material, based on analysis of complete-tree specimens collected from the full range of var. *latifolia* Engelm. in the United States and Canada, and var. *murrayana* (Grev. & Balf.) Engelm. collected from Oregon and California. Compares and correlates with latitude, longitude, elevation, and tree diameter: general tree characteristics, dimensions, moisture contents, weights, cubic volumes, and stem taper; and specific gravity, weight, volume and moisture content of tree components, including heartwood and sapwood, foliage, and wood and bark of roots, stem, and branches. Properties of lodgepole pines vary significantly with latitude, elevation, diameter class, and variety.

KEYWORDS: lodgepole pine, *Pinus contorta*, timber utilization, tree characteristics, wood utilization, timber resource

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